The Macrofossil Record of Proteaceae in Tasmania: a Review with New Species

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Abstract

About ten taxa of Proteaceae are known from the Early Eocene in Tasmania, one from a Late Eocene site, 22 from four Early Oligocene sites, one from a Late Oligocene/Early Miocene site, 12 or 13 from two Early Pleistocene sites, and five or six from the Middle and Late Pleistocene. Most of the Tertiary fossils are of extinct species, but the extant species *Lomatia fraxinifolia* and *Telopea truncata* have been recorded from the Early Oligocene as well as apparent close relatives of the subalpine rainforest species *Orites milliganii*, and the sub-tropical rainforest species, *O. excelsa*. None of the Early Oligocene species are known from more than one site, implying very high regional diversity, and floristic differentiation among the sites. High diversity of Proteaceae at some sites may be associated with oligotrophic soils. There is no evidence of any of the modern species-rich scleromorphic groups of Proteaceae except Banksiinae. Scleromorphy was well established in Oriteae, Embothrieae and Banksiinae by the Early Oligocene. The Early Eocene fossils have very small stomata, sparsely distributed on the leaf, which may have been due to elevated atmospheric CO_2. All extant Tasmanian genera and many extant species were present by the Early Pleistocene as well as some extinct species. The specific diversity within the region was probably higher than it is now.

In order to resolve a nomenclatural problem with the genus *Proteaciphyllum, Euproteaciphyllum* G.J.Jord., R.J.Carp. & R.S.Hill, gen. nov. is proposed and this name is applied to 10 previously described species. The Tasmanian fossil taxa include three new records, and nine new species: *Euproteaciphyllum brookerensis* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., and *E. tasmanicum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. from Early Eocene sediments; and *Orites milliganoides* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., *O. scleromorpha* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., *E. papillosum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., *E. polymorphum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., *E. microlobium* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., *E. falcatum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov., and *E. serratum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. from Early Oligocene sediments.

Introduction

Proteaceae is a diverse family of 79 recognised genera and perhaps 1700 species (Douglas 1995). Australia is the main centre of diversity of the family. South America, South-East Asia, Madagascar and the South Pacific each contain several genera. One subfamily, Proteoideae, has diversified in the Cape Province of South Africa. Proteaceae can be divided reasonably clearly into rainforest and non-rainforest species (Table 1; Johnson and Briggs 1975). The non-rainforest species are almost all highly scleromorphic and most tropical and subtropical rainforest species are more mesomorphic, but cool temperate and montane rainforest species are often highly scleromorphic. Almost all non-rainforest species occur in oligotrophic habitats, and most occur in seasonally very dry habitats. There are many non-rainforest species, but relatively few rainforest species (Table 1). In contrast, at higher taxonomic levels there are more rainforest taxa than non-rainforest taxa (Table 1; Johnson and Briggs 1975). This contrast is due to the occurrence of a number of small, highly relictual rainforest genera, and the diversification of several genera in scleromorphic vegetation (e.g. *Grevillea*, *Hakea*, *Persoonia*, *Banksia*, *Dryandra*, *Conospermum* and *Synaphea* all have 50 or more species in scleromorphic vegetation: Wrigley and Fagg 1991; McCarthy 1995). Johnson and Briggs (1975) considered that the rainforest habitat is likely to have been ancestral in the Proteaceae because many primitive taxa in the family are restricted to rainforest.

Proteaceae have a long and relatively rich fossil record (Hill *et al*. 1995), although most studies of Proteaceae macrofossils have concerned the tribe Banksieae (e.g. Cookson and Duigan 1950; Christophel 1984; Hill and Christophel 1988; Carpenter *et al*. 1994*b*). Macrofossils of other Proteaceae are common, but until recently few have been formally recorded (e.g. Carpenter and Hill 1988; Carpenter and Jordan 1997). Palynomorphs of Proteaceae were particularly diverse, and dominated south-eastern Australian palynofloras in the Palaeocene and Eocene, with many taxa disappearing at about the end of the Eocene (Hill *et al.* 1995; Macphail *et al.* 1994). Dettmann and Jarzen (1991) used the pollen record to imply that many of the rainforest lineages, and at least some of the scleromorphic lineages, had differentiated by the Late Cretaceous. Their evidence is somewhat ambiguous because of long gaps in the fossil record of some taxa, leaving the possibility that the similarity of some fossil pollen to modern species may be due to convergence (Hill *et al*. 1995). Macrofossils may be of use in determining whether the early Tertiary diversity of Proteaceae was due to the presence of extant taxa, or extinct lineages. Macrofossils may also be useful in determining the history of extant groups of Proteaceae and the history of scleromorphy, in particular the timing of its origin in various groups.

Carpenter and Jordan (1997) discussed aspects of Early Tertiary proteaceous diversity in Tasmania based on the Cethana site. That discussion will be extended here to the whole Cenozoic, and will include further discussion of leaf form and palaeoecology. Tasmania is used as a case study because it is a small, discrete geographic unit, and well-preserved macrofossils of Proteaceae are reasonably common there (e.g. Carpenter *et al*. 1994*a*; Jordan 1995*a*; Carpenter and Jordan 1997). Well-preserved and diverse Cenozoic Proteaceae pollen also occur in the region (Macphail *et al.* 1993*a*, 1993*b*; 1994). The record is dominated by leaf fossils with preserved cuticle because it is difficult to assign leaf impressions to the family with confidence, and little is known of proteaceous fossils of wood, fruit or flowers from Tasmania.

Methods

Fossil Sites

Figure 1 and Table 2 show the localities and ages of the Tasmanian Cenozoic sites referred to in this work. Ages follow the scale of Harland *et al*. (1990).

The three sites from which new species of Proteaceae are described are Brooker, Lea River and the Lemonthyme core. The Brooker site was dated palynostratigraphically by M. K. Macphail (personal communication) as Early Eocene and some macrofossils were mentioned by Carpenter *et al*. (1994*a*). The site is an exposure of mudstones and sandstones in a road cutting near Hobart (42°14' S, 147°14' E, 80 m above sea level). Material containing compressions and impressions of leaves was collected in 1992. Only about 20 specimens with cuticle are available and further

material and stratigraphic information will be difficult to obtain because of road works. The Lea River site was briefly described by Hill *et al*. (1993), and palynostratigraphy indicates that it is of Early Oligocene age (M. K. Macphail personal communication). The Early Oligocene Lemonthyme Creek core was described by Macphail *et al*. (1993*a*). Being a core, the samples may cover a significant time range, but the pollen flora is relatively constant throughout the sample (Macphail *et al*. 1993*a*).

Other Tasmanian sites from which Proteaceae macrofossils are known have all been dated palynostratigraphically (Table 2; see Macphail *et al.*. 1994 for a discussion of the palynostratigraphy). Note that the Regatta Point sediments include Early Eocene, Early Pleistocene and Early-Middle Pleistocene sediments.

Fossil Identification, Nomenclature and Terminology

Terminology for cuticles follows Dilcher (1974). Where stomata are restricted to one leaf surface, these leaves are assumed to be hypostomatous, because no extant Proteaceae is epistomatous, and several of the fossils described here have features which are consistent with hypostomaty. These features include leaves with narrowly recurved margins and a midrib which is concave near the leaf base on the non-stomatiferous surface. Classification of extant members of the family follows Douglas (1995).

Carpenter and Jordan (1997) proposed the form genus *Proteaciphyllum* for fossil leaves and cuticle which can be confidently assigned to Proteaceae. However, this name is illegitemate, because it was used earlier by Macginitie (1974) for impressions of some organs which may be petals, sepals, phyllodes or leaves, and which may or may not be Proteaceae. Therefore, a new genus, *Euproteaciphyllum* for the taxa described by Carpenter and Jordan (1997) as *Proteaciphyllum*.

Members of *Euproteaciphyllum* have brachyparacytic stomata, trichomes leaving a rounded scar on the epidermis and at least some trichome bases overlying more than one basal epidermal cell. Most extant Proteaceae have this distinctive combination of features, and it is unknown in any other family (Blackburn 1981; Carpenter 1994; Carpenter and Jordan 1997), including the likely sister group of Proteaceae, Platanaceae (Chase *et al*. 1993). Some extant Proteaceae do not have these features (e.g. *Bellendena montana* R. Br. does not have brachyparacytic stomata and many Proteoideae do not have trichomes with more than one basal epidermal cell), but may have other distinctive features which can be used to assign some fossils to extant groups within the family. Proteaceae often also have unusual leaf forms, although similar forms may occur in other families.

Described fossils from the literature are considered, and some previously undescribed taxa are identified using leaf architecture, cuticular morphology and in some cases, leaf anatomy. Comparisons were made with a large collection of extant Proteaceae cuticles containing all recognised genera, and a total of about 400 species (see Carpenter and Jordan 1997). Where possible apparently apomorphic features were used to assign fossils to extant taxa. Cuticles of samples were prepared by taking small samples of the organic leaf material, immersing them in 30% HF for about two h, then immersing them in 10% aqueous Cr_2O_3 or dilute H_2O_2 with a small amount of tetra sodium pyrophosphate, until tissues other than cuticle had oxidised and dissolved, then staining the remaining cuticle with Safranin O. After mounting on slides in glycerin jelly, cuticle fragments were observed and photographed with transmitted light microscopy. Cuticle fragments were observed with scanning electron microscopy using an Electroscan ESEM 2020 scanning electron microscope operating at 15 kV under high vacuum mode after gold coating to a thickness of approximately 20 nm.

Distinctive hypodermi were preserved in some of the fossils. These were extracted in the process of cuticle preparation. Transverse sections of a range of Proteaceae were prepared to assess the distribution of hypodermi within the family. These included all recognised species of *Orites*, *Neorites* and members of all other tribes of Proteaceae, with emphasis on scleromorphic species of tribes. Sections of over 100 species were examined. For Tasmanian species, both glasshouse grown and field specimens were sectioned, and these different conditions had no affect on the presence or absence of hypodermi, although there were some differences in the degree of thickening

of hypodermal cell walls. Since glasshouse conditions are mesic and warm, and the field habitats of many of these species are extreme (e.g. the sections of all the Tasmanian *Orites* species included specimens from exposed alpine conditions) it is likely that the presence or absence of these hypodermi is genetically fixed within species, and hence useful taxonomically. Hypodermi were extracted from some extant species by immersing leaf fragments in hot H_2O_2 with a small amount of tetra sodium pyrophosphate until the mesophyll could be removed.

Stomatal Lengths

Stomatal lengths of extant and fossil Proteaceae were measured as the length from stomatal pole to pole using an eyepiece graticule at x640 magnification on an Zeiss Axioskop microscope. Lengths of three or four stomata of each extant cuticle sample, and about 10 of each fossil were measured. This was considered sufficient because the variation in stomatal size within cuticle samples was small compared to differences between species. All extant species in the collection of Proteaceae (see above) were measured.

Results

Table 2 lists all records of leaves and fruit from Cenozoic Tasmania that have been demonstrated to be Proteaceae at the time of preparation of this paper. Nine new species are proposed. In addition there are new records of Proteaceae. Cuticle fragments from the Buckland sediments (Figs 30, 31) differ from the cuticle of *Euproteaciphyllum brookerensis* G.J.Jord., R.J.Carp. & R.S.Hill (described below) only in having strong striations of the stomatiferous surface. Other fragments of the cuticle of the non-stomatiferous surface from this site have larger epidermal cells than the first taxon and have undulate anticlinal walls (Fig. 32), but at present they are not treated as a second taxon. At least one species of Proteaceae occurs in the Monpeelyata sediments (Figs 83-85). The cuticles are poorly preserved, and it is difficult to determine the affinities with confidence, except to say that they are distinct from those of any other known fossil of Proteaceae from Tasmania.

Excluded Species

Several species of *Banksieaephyllum* are unlikely to be proteaceous because their trichome bases are unlike those of any extant Proteaceae, and some specimens have stomata which appear not to be brachyparacytic (Carpenter and Jordan 1997; R. J. Carpenter unpublished data). Two undescribed taxa from Cethana (Carpenter 1991) and one specimen from Lemonthyme Creek, *B. aberensis* R.S.Hill & Christophel from the Middle-Late Eocene Loch Aber site (Hill and Christophel 1988) and *B. regularis* R.S.Hill & Christophel from the Late Oligocene-Early Miocene Pioneer sediments (Hill and Christophel 1988) are excluded on this basis. Johnston (1888) mentions Tertiary fossil leaves of *Lomatia praelongifolia* Ett. and *Dryandroides johnstonii* Ett., but there is no evidence that any of these fossils had cuticular preservation. Johnston (1874) identified petrified wood from Corra Lynn, northern Tasmania, as *Banksia*. This has not been confirmed, although this wood is proteaceous because of its distinctive wood.

Systematics

Family Proteaceae

Orites R.Br.

***Orites milliganoides* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 2-8)**

Diagnosis

Leaf small, obovate, with few teeth. Multiseriate adaxial hypodermis of elongate sclerenchyma cells, 1-2 seriate abaxial hypodermis of short, scarcely thickened cells arranged tangentially around stomata to form a reticulum. Epidermal cells almost isodiametric, about half the length of the subsidiary cells or less, stomata longer than broad.

Description

Leaf obovate, about 22 mm by 12 mm, slightly asymmetric, slightly concave adaxially, each side

with a single acuminate/acute tooth, hypostomatous. Apex acuminate. A strong vein leading to each tooth, and weaker veins looping to the next secondary vein; secondary veins diverging from midrib at moderate-high angles. Outer surfaces of cuticle not ornamented. Epidermal cells of adaxial surface 4-6 sided, nearly isodiametric, about 20-30 by 25-40 µm, cuticle thick except for the thin, even anticlinal walls; trichome bases occasional on adaxial surface, elliptical, typically 50-70 by 25 µm, overlying 2 (-3, rarely 4) enlarged (about 50-60 µm) epidermal cells. Epidermal cells of abaxial surface more isodiametric and smaller (20-25 µm) than those of adaxial surface, anticlinal walls evenly thickened. Stomata brachyparacytic, large, about 60 µm long by 40 µm broad, more or less aligned with the long axis of the leaf; guard cells about 20-25 µm wide; subsidiary cells about as long as stomata, about 10-15 µm wide; guard cells and subsidiary cells darker staining than epidermal cells; outer cuticular ledges prominent, but in the same plane as the general cuticle surface, cuticle above subsidiary cells depressed. Trichome bases of abaxial surface occasional, similar to those of adaxial surface, except overlying 3-6 slightly enlarged epidermal cells. Multiseriate hypodermis of elongate sclereids present adaxially; 1-3 seriate hypodermis present abaxially, of short, scarcely thickened cells arranged tangentially around stomata to form a reticulum.

Holotype: Lea2746, stored in the Department of Plant Science, University of Tasmania.

Type Locality: Early Oligocene sediments on the Lea River, north-western Tasmania.

Other specimens examined: Lea2753, Lea2747, Lea2748.

Etymology: To reflect its close affinity to the extant species *O. milliganii*.

Discussion:

Orites milliganoides is based on four leaves from the Lea River deposit. It is clearly related to *O. milliganii* and *O. acicularis* from which it differs only in leaf shape and some cuticular features discussed below. Figure 9 illustrates the range of variation in leaf form within *O. milliganii*, *O. acicularis* and a putative hybrid between these species. *Orites milliganoides* differs from *O. milliganii* (Fig. 9-11; also illustrated by Carpenter and Jordan 1997) in having only few teeth, elongate stomata, many trichome bases on the adaxial lamina and larger adaxial epidermal cells. *Orites acicularis* (Figs 9, 12 and 13) differs from *O. milliganoides* in having acicular leaves with the adaxial leaf surface reduced to a narrow band.

The features most strongly linking *Orites milliganoides* to *O. milliganii* and *O. acicularis* are the distinctive, strongly sclerified hypodermi. The abaxial hypodermi are 1-2 seriate, sclerified, and made up of narrow, slightly elongated cells. The cells are arranged around each stoma, forming a reticulum which is independent of the veins (Fig. 8). This feature appears to be a synapomorphy for *O. milliganoides*, *O. milliganii* (Fig. 11), *O. acicularis* and a putative hybrid between the latter two species because a survey of a wide range of extant Proteaceae, including both rainforest and scleromorphic taxa found no other similar hypodermi. It is not certain that *O. milliganii* and *O. acicularis* form a clade within *Orites*, but these species apparently hybridise (George and Hyland 1995), and have similar cuticles and leaf anatomy, apart from features related to the reduction of the adaxial surface in *O. acicularis*. Some species, notably *Eidothea zoexylocarya* A.W.Douglas & B.Hyland, have abaxial sclerified hypodermal cells, but they are uniseriate and are similar in form to the mesophyll cells. Many *Banksia* and *Dryandra* species have sclerenchyma connecting the veins with the abaxial epidermis forming a reticulum (Cookson and Duigan 1950) but this is clearly distinct from the hypodermis in the *O. milliganii* group, because each areole encloses many stomata. The adaxial hypodermi of *O. milliganoides* (Fig. 7) and *O. milliganii* (Fig. 10) and the putative hybrid are multiseriate, and made up of elongate, moderately thickened cells. The extreme reduction of the adaxial surface of *O. acicularis* means that it is not possible to detect an adaxial hypodermis. *Banksia* and *Dryandra* also have multiseriate adaxial hypodermi. Uniseriate adaxial hypodermi occur in *O. diversifolia* R.Br. and *O. lancifolia* F.Muell., a 1-2 seriate adaxial

hypodermis occurs in *O. revoluta* R.Br., and in *E. zoexylocarya* there is a uniseriate adaxial hypodermis made up of sclerified mesophyll cells. No hypodermi were found in the other Proteaceae surveyed, although some had sclerification of the uppermost mesophyll cells and others had isolated sclereids in the mesophyll.

Some cuticular features shared by the fossils and *O. milliganii* include epidermal cells which are considerably smaller than the stomata, unornamented cuticles, and stomata which are depressed so that the outer cuticular ledges are on the same plane as the general cuticle surface (see Carpenter and Jordan 1997). These features also occur in some other Proteaceae, including fossils described below, but not in *Banksia* or *Dryandra*, the only genera apart from *Orites* with multiseriate hypodermi.

***Orites scleromorpha* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 14-21)**

Diagnosis

Leaves small, linear, sparsely and finely serrate. Multiseriate adaxial hypodermis of elongate sclerenchyma cells, 1-2 seriate abaxial hypodermis of short, scarcely thickened cells arranged tangentially around stomata to form a reticulum. Epidermal cells almost isodiametric, less than half the length of the subsidiary cells, stomata scarcely longer than broad.

Description

Leaves hypostomatous, linear, about 4-8 mm broad, up to at least 40 mm long, with frequent, small, irregularly spaced, rounded, apically directed teeth along both margins; base rounded-acute. A strong vein leading to each tooth, and weaker veins looping to the next secondary vein; secondary veins diverging from midrib at moderate angles. Adaxial surface smooth; trichomes restricted to midrib and leaf margins; epidermal cells more or less isodiametric, typically about 25-30 µm, with straight, evenly thickened anticlinal walls; trichome bases elliptical or rounded, typically about 50 µm long, mostly overlying 2-many epidermal cells; basal epidermal cells similar to epidermal cells, except often more elongate. Abaxial surface smooth; epidermal cells smaller than those of adaxial surface, typically about 16-20 by 18-25 µm, anticlinal walls thick; trichome bases occasional, similar to those of adaxial surface. Stomata brachyparacytic, randomly oriented, more or less uniformly distributed across lamina; pair of guard cells forming an almost circular ring 45-55 µm long, 40-50 µm broad; subsidiary cells narrow, about 5 µm wide; outer cuticular ledges prominent, but in the same plane as the general cuticle surface with the cuticle above subsidiary cells depressed. Multiseriate hypodermis of elongate sclereids present adaxially; 1-2 seriate hypodermis present abaxially, of short, scarcely thickened cells arranged tangentially around stomata to form a reticulum.

Holotype: Lea1554 stored in the Department of Plant Science, University of Tasmania.

Type Locality: Early Oligocene sediments on the Lea River, north-western Tasmania.

Other specimens examined: Lea1757, Lea1758, Lea2749-Lea2753.

Etymology: To reflect the highly scleromorphic form and anatomy of the leaf.

Discussion:

Orites scleromorpha is represented by several morphologically similar specimens (Figs 14-21). Like *O. milliganoides*, it is clearly closely related to *O. milliganii* and *O. acicularis*. The cuticular morphology (Figs 15-19) is almost identical to that of *O. milliganii* and it shares the distinctive hypodermi (Figs 20 and 21). It differs markedly from *O. milliganii*, *O. acicularis* and *O. milliganoides* in that the leaves are linear, with sparse, small teeth (Fig. 14). It also differs from *O. milliganoides* in having non-elongate stomata, few trichome bases on the adaxial lamina and smaller adaxial and abaxial epidermal cells It is possible that *O. scleromorpha* and *O. milliganoides* were variants of one species (possibly due to heteroblasty), but the interpretation that

they were different species is preferred because the difference in leaf form is greater than the variation within the related extant species (Fig. 9).

Euproteaciphyllum G.J.Jord., R.J.Carp. & R.S.Hill, gen. nom. nov., based on *Proteaciphyllum* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 553 (1997)), nom. illeg., non Macgintie (1974).

Leaves or dispersed cuticles with paracytic stomates. Trichome bases overlying one or more epidermal cells, leaving a rounded scar on the cuticle. At least some trichome bases overlying more than one epidermal cell.

Type species: Euproteaciphyllum tridacnoides

Etymology

The name implies that these fossils are true leaves of Proteaeceae.

Euproteaciphyllum tridacnoides G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum tridacnoides* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 554 (1997)), nom. illeg.

Euproteaciphyllum lomatioides G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum lomatioides* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 554 (1997)), nom. illeg.

Euproteaciphyllum gevuininoides G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum gevuininoides* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 554 (1997)), nom. illeg.

Euproteaciphyllum cethanicum G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum cethanicum* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 557 (1997)), nom. illeg.

Euproteaciphyllum linearis G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum linearis* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 557 (1997)), nom. illeg.

Euproteaciphyllum rugulatum G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum rugulatum* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 557 (1997)), nom. illeg.

Euproteaciphyllum attenuatum G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum attenuatum* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 558 (1997)), nom. illeg.

Euproteaciphyllum ornamentalis G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum ornamentalis* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 558 (1997)), nom. illeg.

Euproteaciphyllum integrifolium G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum integrifolium* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 558 (1997)), nom. illeg.

Euproteaciphyllum microphyllum G.J.Jord., R.J.Carp. & R.S.Hill, nom. nov., based on *Proteaciphyllum microphyllum* R.J.Carp. & G.J.Jord. (Australian Systematic Botany 10: 559

(1997)), nom. illeg.

***Euproteaciphyllum brookerensis* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 22-28)**

Diagnosis

Leaves pinnately lobed to within about 1 mm of midrib, lobes falcate with a few teeth. Outer surface of adaxial cuticle strongly striated, striations radiating from trichome bases. Trichome bases abundant, associated with up to 6 basal epidermal cells. Stomata with prominent outer cuticle ledges raised well above cuticle surface, with a narrow aperture.

Description

Leaves hypostomatous, pinnately lobed to within about 1 mm of the midrib. Lobes linear falcate, occurring at about 6-9 mm intervals, typically 15-30 mm long, 3-3.5 mm broad in the midlobe; basal portion of lobe decurrent down the midrib, lobe apex rounded, mucronulate. Venation of lobes brochidodromous, secondary veins departing from midrib at about 50-70°, veins leading from the loops to the occasional teeth, higher order veins reticulate. Upper margin of lobes with 2-6 very small, rounded, distally pointed teeth; lower margin entire or with 1-2 similar teeth. Midrib prominent, convex abaxially, grooved adaxially, margins slightly thickened abaxially.
Epidermal cells more or less isodiametric with slightly undulate or nearly straight anticlinal walls, about 20-25 µm adaxially, slightly smaller (20 µm) abaxially. Trichome bases frequent, nearly circular, about 20 by 15 µm, usually overlying only one slightly enlarged, rounded epidermal cell, typically 25-30 µm diameter, occasionally trichome bases overlying up to 6 cells; periclinal wall of basal epidermal cells darker staining in safranin O than those of other epidermal cells. Outer surface of cuticle prominently striated adaxially, with striations radiating from trichome bases. Stomata small, randomly aligned, brachyparacytic, more or less evenly distributed across the leaf; outer cuticular ledges of stomata protruding from leaf surface, with a narrow aperture; guard cells about 20 µm long, forming an almost circular torus; subsidiary cells light staining.

Holotype: BH1, stored in the Department of Plant Science, University of Tasmania.

Type locality: Early Eocene sediments on the Brooker Highway, near Hobart.

Other specimens examined: BH3, BH13, BH15.

Etymology: Named for the type locality.

Discussion

Euproteaciphyllum brookerensis is based on a few specimens of deeply lobed leaves with distinctive striated cuticle (Figs 22-28) from the Early Eocene Brooker sediments. It has brachyparacytic stomata and trichome bases typical of Proteaceae and the cuticular features of subfamily Grevilleoideae, but it cannot be confidently assigned to an extant genus. Extant Grevilleoideae which have deeply lobed leaves of this general size and form occur in several groups, including *Grevillea*, *Lomatia* and subtribe Banksiinae (*Banksia* and *Dryandra*). The fossils differ from Banksiinae in having lobes with teeth. Also, almost all Banksiinae have trichomes with cylindrical bases and most have stomata restricted to areoles (Cookson and Duigan 1950; Hill and Christophel 1988). The striated cuticles of the fossils, with stomata protected by outer cuticular ledges raised well above the level of the epidermis, are unlike extant *Grevillea* or *Lomatia* species, although in other aspects the cuticles are consistent with some *Lomatia* species (see Carpenter and Hill 1988; Carpenter 1994). The general leaf architecture of the fossils, including venation, is consistent with *Lomatia*, especially some forms of *L. fraseri* R.Br. (Fig. 29). *Euproteaciphyllum brookerensis* resembles no other species of *Euproteaciphyllum*. In particular, neither of the two previously described species with deeply divided leaves, *E. lomatioides* and *E. tridacnoides* from Cethana, have striated cuticle, and both have a densely hairy abaxial surface and much larger stomata than *E. brookerensis*. *Euproteaciphyllum tridacnoides* also has stomata which are

protected by remarkable cuticular extensions.

Euproteaciphyllum tasmanicum **G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 33-40)**

Diagnosis

Leaf hypostomatous with very small, sparse teeth. Stomata smaller than epidermal cells, subsidiary cells usually unevenly sized, epidermal cells small. Trichome bases small, usually about 15 µm wide, overlying 1, occasionally 2 slightly enlarged basal epidermal cells, not differentially staining.

Description

Leaf/leaflet/lobes hypostomatous, linear, asymmetric, about 20 mm wide, at least 35 mm long, sparsely serrate on both margins; teeth very small, rounded, apically directed. Venation semicraspedodromous. Epidermal cells 20-40 by 15-30 µm, with undulate or straight, evenly thickened, anticlinal walls. Trichome bases common, obscure, elliptical to circular, typically 15 µm wide, up to about 25 µm long, mostly overlying one, occasionally two, slightly enlarged basal epidermal cells with straight, unevenly thickened anticlinal walls. Adaxial surface with longitudinal striations along veins, radial striations around trichome bases. Stomata mostly aligned with the long axis of the leaf, brachyparacytic, smaller than epidermal cells; pair of guard cells 15-20 µm long, as broad as long, prominent T-shaped pieces of cuticle at the poles; subsidiary cells of variable width, when narrow usually associated with a single epidermal cell, outer cuticular ledges weakly developed.

Holotype: BH11, stored in the Department of Plant Science, University of Tasmania.

Type locality: Early Eocene sediments on the Brooker Highway, near Hobart.

Other specimens examined: BH5, BH6.

Etymology: To recognise a new Tasmanian species.

Discussion:

Euproteaciphyllum tasmanicum is based on three leaf fragments from the Brooker site (Figs 33-38). Because of their asymmetry, the fragments may be parts of leaflets. It differs from *E. brookerensis* in having larger leaflets, smaller stomata with much less prominent outer cuticular ledges (Fig. 36), and inconspicuous trichome bases which overlie only one or two basal epidermal cells (Fig. 38). The subsidiary cells tend to be unevenly sized and almost always share a long anticlinal wall with an epidermal cell. Large subsidiary cells tend to resemble the epidermal cells in having thicker, sometimes undulate anticlinal walls. This gives the appearance that after the differentiation of the guard cells, subsidiary cells often divide along a longitudinal plane to produce one cell like a normal proteaceous subsidiary cell, and another more like an epidermal cell. Some *Stenocarpus* and *Lomatia* species have similar structures (see Carpenter 1994). In most other Grevilleoideae and most Persoonioideae, there is no clear association between the subsidiary cells and the adjacent epidermal cells (e.g. Fig. 20). One specimen (BH5) differs from the type in having thinner cuticle, fewer stomata, and larger epidermal cells with undulate anticlinal walls (Figs 39, 40). This may be a variant of the species, perhaps a shade leaf, although it could be a different species. Such a degree of variation occurs within extant species of *Lomatia* and *Stenocarpus*. Although *E. tasmanicum* has some features in common with *Lomatia* and *Stenocarpus*, these features appear to be fairly generalised within the family and no close affinity is implied. Also, *E. tasmanicum* lacks trichome bases associated with more than two basal epidermal cells, and does not have clearly granular subsidiary cells, so its tribal affinity is unclear.

Euproteaciphyllum papillosum **G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 41-50)**

Diagnosis

Leaves entire, margins recurved. Abaxial surface with prominent epidermal papillae. Epidermal

cells of adaxial surface with undulate anticlinal walls.

Description

Leaves hypostomatous, linear, entire, about 6 mm wide, at least 60 mm long, midrib prominent on both surfaces, about 1 mm wide, margins narrowly recurved.

Adaxial surface with epidermal cells with undulate, evenly thickened anticlinal walls; trichome bases circular to elliptical, typically 18-25 by 25-45 µm, overlying 4-many (≥10) basal epidermal cells with straight, unevenly thickened, anticlinal walls; groups of basal epidermal cells typically 50 by 60 µm, slightly larger than trichome bases. Outer surface of adaxial cuticle smooth apart from trichome bases. Abaxial surface with epidermal cells more or less isodiametric, typically 20 µm across, with thick anticlinal walls forming a rounded lumen, each cell projecting abaxially to form a prominent papilla, outer cuticle thickened to form a protuberance on the end of each papilla. Stomata and trichome bases at the same level as the epidermal cells. Stomata randomly oriented, more or less evenly distributed across the abaxial lamina, with prominent outer cuticular ledges, brachyparacytic, larger than the epidermal cells. Trichome bases smaller and with fewer basal epidermal cells than those of adaxial surface.

Holotype: Lea1762, stored in the Department of Plant Science, University of Tasmania.

Type Locality: Early Oligocene sediments on the Lea River, north-western Tasmania.

Etymology: To emphasise the papillose abaxial surface.

Discussion

Euproteaciphyllum papillosum is based on one specimen from the Early Oligocene Lea River sediments (Figs 41-46). It is an entire margined linear leaf or leaf lobe, with revolute margins and a stomatiferous surface with prominent papillae mainly formed by extensions of the lumens of the epidermal cells. Similar papillae occur in several extant species of Grevilleoideae including *Orites diversifolia* (Tribe Oriteae), *Telopea truncata*, *Embothrium coccineum* J.R.Forst. & G.Forst., *Lomatia ferruginea* (Cav.) R.Br. (Figs 47-50; Tribe Lomatieae), and *Kermadecia pronyensis* (Guillaumin) Guillaumin (Tribe Macadamieae). The fossil's papillae differ from those in the extant species in that the outer periclinal of each epidermal cell appears to be approximately in the same plane as the stomata apart from a central extension forming the papilla. In the extant species with epidermal papillae the whole periclinal wall forms the papilla. The fossils differ from *E. coccineum* in having the pair of outer cuticular ledges of each stoma prominent and raised (see Carpenter and Jordan 1997). Unlike *E. coccineum*, *T. truncata*, *O. diversifolia* and *K. pronyensis*, the epidermal cells of the adaxial surface of *E. papillosum* have undulate anticlinal walls (Figs 44, 46). *Kermadecia* species have striated subsidiary cells, and *K. pronyensis* has strongly striated adaxial epidermis with striations on the papillae. *Lomatia* species, including *L. ferruginea* (Fig. 49), often have epidermal cells with undulate anticlinal walls like those of the fossils, but no extant *Lomatia* species has striated cuticles. Thus, although *E. papillosum* is a distinctive taxon, its affinities within Grevilleoideae are unclear.

***Euproteaciphyllum polymorphum* G.J.Jord., R.J.Carp. & R.S.Hill, sp. nov. (Figs 51-60)**

Diagnosis

Leaves hypostomatous, pinnatisect or pinnatifid apart from lobed apical portion, proximal part of the apical margin of leaflets almost parallel to midrib, basal margin decurrent down stem, decurrent part sometimes apparently extending beyond the attachment of the adjacent leaflet. Trichome bases circular or nearly so, about 25-35 µm diameter, overlying 2-10 basal epidermal cells forming a complex up to 90 µm in diameter. Stomata brachyparacytic, one or two subsidiary cells with a transverse septum.

Description

Leaves hypostomatous. Apical portion deeply lobed, other portions pinnatisect, or almost regularly pinnatifid. Leaflets diverging from midrib at about 45-70°, at about 10 mm intervals along midrib, falcate, 15-30 mm long, 4-15 mm broad at the widest point about 1/3 along the leaflet, proximal portion of leaflet tapering to a thickened base about 2 mm broad, basal margins decurrent down stem, often forming a rib extending beyond and abaxially of adjacent leaflet, apical margins almost parallel to midrib for up to 10 mm, attaching to near the centre of the midrib, in some specimens leaflets overlapping both the midrib and adjacent lobes. Leaflets with up to six, unevenly spaced, small, distally facing teeth on the apical side, none to a few similar teeth on the basal side. Leaflet apices acute or obtuse.

Epidermal cells more or less isodiametric, 4-6 sided, 15-25 by 20-30 µm, with smooth, straight anticlinal walls on adaxial surface, beaded, slightly undulate anticlinal walls on abaxial surface. Trichome bases occasional on adaxial surface, apparently absent from abaxial surface, circular to slightly elliptical, 25-30 µm, overlying 2-10 dark staining epidermal cells forming a group usually 1.25 to 1.33 times as long as the trichome base. Stomata common and more or less evenly distributed on abaxial surface, randomly oriented, brachyparacytic; guard cell pair larger than epidermal cells about 30-35 µm long, as broad as long; subsidiary cells narrow, about 5 µm wide, sometimes with transverse septa; outer surface of cuticle depressed above subsidiary cells so that the prominent outer cuticular ledges are on the same plane as the general cuticle surface.

Holotype: LT330 (LT337 is the counterpart), stored in the Department of Plant Science, University of Tasmania.

Type locality: The Early Oligocene Lemonthyme Creek sediments, north-western Tasmania.

Other specimens examined: LT007, LT022, LT137, LT220, LT305, LT343, LT344.

Etymology: To reflect the great variation in lobe form.

Discussion

Euproteaciphyllum polymorphum is based on a number of pinnatisect or deeply lobed specimens from Lemonthyme Creek (Figs 51-60). The specimens show a wide range in gross morphology (Figs 51-55). This range may represent different parts of leaves, leaves from different developmental stages or leaves which developed under different conditions. It is possible that more than one biological species with similar cuticle may have been present, but there appears to be a continuum in form. At one extreme of this range the laminae of the lobes overlap each other and the midrib (Fig. 55), which is unlike any living Proteaceae. Another distinctive feature is that the lower (i.e. towards the leaf base) margin of each leaflet is decurrent down the stem and often appears to become fused to the stem and extend past the next leaflet down the midrib, because the upper margin is attached near the centre of the midrib (Figs 52, 53). It appears that the leaflets were attached obliquely to the midrib. Apart from these features, the leaf architecture is consistent with some *Lomatia* species (Fig. 29). Most stomata are clearly brachyparacytic, and conform exactly to the general form of Proteaceae stomata, but in some there appear to be two subsidiary cells exactly where one would normally be (Fig. 57). This suggests either that one of the subsidiary cells has divided after the guard cells has differentiated, or that the apparent wall is a septum only partially dividing the cell. *Bellendena montana* is an extant Proteaceae which is not clearly paracytic. This may not be homologous to the division of the subsidiary cells in *E. polymorphum* because it is not as obviously the result of partition of subsidiary cells (Fig. 61). The combination of leaf architecture, trichome bases, and all other aspects of stomatal morphology indicate that the fossil is Proteaceae.

Euproteaciphyllum microlobium **G.J.Jord., R.J.Carp. and R.S.Hill, sp. nov. (Figs 62-68)**

Diagnosis

Leaves hypostomatous, more or less regularly pinnately lobed to within about 1 mm of midrib.

Lobes small linear-falcate, about 2 mm broad at midlobe, placed at about 4 mm intervals. Trichome bases large, typically 50 µm long. Stomata randomly aligned, stomatal complex similar in size to epidermal cells.

Description
Leaves hypostomatous, deeply lobed. Lobes entire margined, reaching to within about 1 mm of midrib, linear-falcate, lobe axes at about 50° to midrib, about 10-12 mm long, 2 mm wide at midlobe, placed at about 4 mm intervals, basal portion decurrent down midrib. Midrib channelled adaxially, convex abaxially.
Leaf surface weakly striated on abaxial surface. Epidermal cells more or less isodiametric, 20-30 µm by 25-30 µm on adaxial surface, 20-35 µm by 25-40 µm on abaxial surface, anticlinal walls nearly straight, evenly thickened. Trichome bases rare on adaxial surface, apparently absent from abaxial surface, elliptical-circular, typically 50 µm long, overlying 2-4 large epidermal cells forming a group up to 80 µm in diameter. Stomata brachyparacytic, not large compared to epidermal cells, 25-30 µm long, about as broad as long; outer cuticular ledges prominent, raised above leaf surface, T-shaped pieces of cuticle at stomatal poles; subsidiary cells very narrow, sometimes not apparent in cuticle preparations.

Holotype: LT310, stored in the Department of Plant Science, University of Tasmania.

Type Locality: The Early Oligocene Lemonthyme Creek sediments, north-western Tasmania.

Etymology: To emphasise the small size of the lobes.

Discussion
Euproteaciphyllum microlobium, is proposed based on one specimen from Lemonthyme Creek. It has much narrower, entire margined lobes, smaller stomata and larger epidermal cells than *E. polymorphum*, and large conspicuous trichome bases (Figs 62-68). No other described species of *Euproteaciphyllum* has such small lobes. *Lomatia xeromorpha* from the Early Oligocene Cethana sediments has narrowly lobed leaves, and shares many cuticular characters with *E. microlobium*, including similar epidermal cells, and a general lack of cuticular ornamentation, but *L. xeromorpha* has small trichome bases, mostly overlying one small, round epidermal cell, whereas *E. microlobium* only has large trichome bases (larger than the epidermal cells), which overly several dark staining epidermal cells (Fig. 68). Also, although the epidermal cells of the two species are of similar size, the stomata of *L. xeromorpha* are distinctly smaller than those of *E. microlobium*. *Lomatia xeromorpha* appears to have some striation associated with veins, which is not present in *E. microlobium*. The leaf architecture of *E. microlobium* is consistent with a number of extant taxa, including some species of *Lomatia*, Banksiinae, *Grevillea* and *Beauprea*. *Euproteaciphyllum microlobium* is consistent with subfamily Grevilleoideae.

***Euproteaciphyllum falcatum* G.J.Jord., R.J.Carp. and R.S.Hill, sp. nov. (Figs 69-76)**
Diagnosis
Leaves serrate with small teeth, hypostomatous, linear-falcate, about 7-12 mm broad. Adaxial leaf surface with striations following veins. Abaxial surface with striations around stomata and radiating from trichome bases. Epidermal cells small, anticlinal walls thickened at cell junctions. Stomata larger than epidermal cells.

Description
Leaves hypostomatous, linear-falcate, irregularly serrate about 7-12 mm wide, at least 40 mm long; teeth small (about 1 mm) apically directed, rounded teeth, apical region tapering gradually. Adaxial leaf surface with striations following veins; abaxial surface with striations around stomata and radiating from trichome bases. Epidermal cells of lamina isodiametric, 15-25 µm, anticlinal walls thick, smooth; epidermal cells of leaf margins and midrib elongate, 20-40 by 10-15 µm.

Trichomes bases rare on adaxial surface, apparently absent from abaxial surface; bases on lamina elliptical-circular, typically 40 µm long, overlying many rounded epidermal cells with very thick anticlinal walls, forming a rounded group of cells about 60 µm diameter; bases on veins elongate, typically 50 by 20 µm, overlying 2-6 basal cells. Stomata brachyparacytic, mostly aligned with long axis of leaf, larger than epidermal cells, typically 35 µm long by 30 µm; T-shaped pieces of cuticle present at stomatal poles, outer cuticular ledges prominent, but in the same plane as the general cuticle surface, cuticle above subsidiary cells depressed.

Holotype: LT214, stored in the Department of Plant Science, University of Tasmania.

Type Locality: The Early Oligocene Lemonthyme Creek sediments, north-western Tasmania.

Other Specimens Examined: LT008, LT017a, LT017b, LT194.

Etymology: To emphasise the falcate leaf shape.

Discussion

Euproteaciphyllum falcatum (Figs 69-76) is based on several serrate, linear-falcate, leaf fragments from Lemonthyme Creek. The only similar described species is *E. microphyllum* from Cethana (Carpenter and Jordan 1997). Like *E. falcatum*, *E. microphyllum* has small serrate linear leaves and stomata which are much bigger than the isodiametric epidermal cells, and which are depressed so that the prominent outer cuticular ledges of the stomata are at the general level of the cuticle. Extant *Orites milliganii* and *O. acicularis* (Figs 12 and 13) also have these cuticular characters (Carpenter and Jordan 1997), but, unlike any extant *Orites* species, *E. microphyllum* and *E. falcatum* have striated cuticles. *Euproteaciphyllum microphyllum* and *E. falcatum* differ in a number of features. The epidermal cells are over twice as long and the stomata of *E. microphyllum* are nearly twice as long as those of *E. falcatum*. Both adaxial and abaxial surfaces of the Lemonthyme Creek fossil are striated (Figs 72, 74). Only the adaxial surface of *E. microphyllum* is striated. Also *E. microphyllum* does not appear to be falcate, and has larger teeth. The striations in *E. microphyllum* are strong, and those *E. falcatum* are weak (Figs 72, 74), although this difference may be due to degradation.

***Euproteaciphyllum serratum* G.J.Jord., R.J.Carp. and R.S.Hill, sp. nov. (Figs 77-82)**

Diagnosis

Leaf apex falcate, tapering evenly, margin sparsely toothed with small, elongate, rounded teeth. Trichome bases large, up to 90 µm long, typically about 35 µm wide, associated with several to many basal epidermal cells. Epidermal cells similar sized to stomatal complex.

Description

Leaf hypostomatous, more than 35 mm long, more than 15 mm wide, with sparse, small, elongate, rounded teeth. Apex tapering more or less evenly.

Leaf surfaces smooth. Epidermal cells of adaxial surface isodiametric or slightly elongate, about 30-50 µm by 20-35 µm, randomly arranged, with evenly thickened, more or less straight anticlinal walls; cells of abaxial surface larger , 30-60 µm by 20-35 µm, with weakly undulate anticlinal walls, granular periclinal walls; cells over veins more elongate. Trichome bases occasional on both surfaces, circular to elliptical or oblate elliptical, typically 3/4 of diameter of group of basal epidermal cells, large, typically 30-45 µm by 40-90 µm, overlying a few to many (>15) basal epidermal cells similar to other epidermal cells, or slightly darker staining; trichome bases over veins more elongate. Stomata more or less uniformly sized; guard cell pair slightly elongate, similar in size to epidermal cells, typically about 40 µm by 30 µm; subsidiary cells with conspicuously granular periclinal walls, narrow, about 5-15 µm wide; outer cuticular ledges prominent, but in the same plane as the general cuticle surface, cuticle above subsidiary cells depressed.

Holotype: LT201, stored in the Department of Plant Science, University of Tasmania.

Type Locality: The Early Oligocene Lemonthyme Creek sediments, north-western Tasmania.

Etymology: To emphasise the sparsely serrate margins.

Discussion

Euproteaciphyllum serratum (Figs 77-82) is based on a single leaf fragment from Lemonthyme Creek with a distinctive tapering leaf apex and sparse elongate teeth. The cuticle of this taxon is distinct from any previously described species of *Euproteaciphyllum*. It is consistent with Grevilleoideae, in particular because it has subsidiary cells with granular periclinal walls (Figs 78, 82). The leaf shape is unusual and does not suggest affinity with any living genus. The cuticular morphology is very generalised for Grevilleoideae, since it does not have any cuticular sculpturing, and the forms of the stomata, epidermal cells and trichomes occur widely in the group. As in some *Orites milliganii* and other *Euproteaciphyllum* species (see above) the stomata are slightly sunken (Fig. 79), so that the stomatal ledges are in the same plane as the general cuticular surface.

Discussion

The History of Taxonomic Groups

Orites

Both mesomorphic rainforest species (*Orites excelsoides*, Carpenter 1994; Carpenter and Jordan 1997) and highly scleromorphic species (*O. milliganoides* and *O. scleromorpha*) of *Orites* have been present in Tasmania since the Early Oligocene. Early Pleistocene sediments (Jordan 1995*a*) contain specimens indistinguishable from distinctive extant Tasmanian species, *O. revoluta* and *O. acicularis*., and of an extinct species related to the extant Tasmanian species, *O. diversifolia*. Fossils identical to the fourth extant Tasmanian species, *O. milliganii*, occur in Early-Middle Pleistocene sediments (Jordan *et al*. 1995).

Lomatia

Two species of *Lomatia* have been recognised from the Early Oligocene Cethana sediments: *Lomatia fraxinifolia* is a mesomorphic, extant, tropical rainforest species (Carpenter and Jordan 1997), whereas *L. xeromorpha* was a scleromorphic similar to extant species of cool, open woodlands (Carpenter and Hill 1988). *Euproteaciphyllum lomatioides* and *E. tridacnoides* from Cethana are also consistent with *Lomatia* (Carpenter and Jordan 1997). *Lomatia* fossils consistent with the extant Tasmanian species *L. tasmanica* W.M.Curtis, and distinct from other extant species, occur in the Late Pleistocene Melaleuca Inlet sediments (Jordan *et al*. 1991). Recent evidence has revealed that *L. tasmanica* is a single ancient clone (Lynch *et al*. in press).

Banksieae

The tribe Banksieae is at least as old as the Late Palaeocene (Carpenter *et al* 1994*b*) but its oldest records in Tasmania are from the Early Oligocene (Carpenter and Jordan 1997; Table 2). One species from this time, *Banksieaephyllum orientalis*, is consistent with the sub-tribe Banksiinae, containing *Banksia* and *Dryandra* (Carpenter and Jordan 1997). Another, *Banksieaephyllum linearis* has some cuticular features that are more consistent with the extant rainforest genus *Musgravea*, but is scleromorphic (Carpenter and Jordan 1997).

Two or three extinct species of *Banksia* occur in Pleistocene sediments in Tasmania (Table 2). *Banksia strahanensis* occurs in the Early Pleistocene Regatta Point sediments, and *B. kingii* occurs in Late Pleistocene sediments at Melaleuca Inlet (Jordan and Hill 1991). *Banksia* cf. *kingii*, from the Regatta Point sediments, may be *B. kingii*, or another extinct species (Jordan 1995*a*).

Other extant groups

The extant species, *Telopea truncata*, occurs in Early Oligocene and Pleistocene sediments (Table 2). A globally extinct species of *Telopea*, *T. strahanensis*, and another which is at least regionally extinct are also known from the Early Pleistocene (Table 2). *Cenarrhenes* is recorded from the Middle-Late Eocene (Pole 1992), although Carpenter and Jordan (1997) considered that this fossil was also consistent with *Beauprea*. *Cenarrhenes nitida* leaves are known since the Early Pleistocene (Jordan 1995*a*), and endocarps are known from the Middle Pleistocene (Fitzsimons *et al*. 1990). *Agastachys odorata* has been in Tasmania at least since the Early Pleistocene (Table 2). The oldest known macrofossils of *Hakea* are from the Early Pleistocene of Tasmania (Jordan 1995*a*). Like all Tasmanian extant *Hakea* species the fossils have needle-like leaves with stomata encrypted by cone-like extensions of epidermal cells. *Euproteaciphyllum gevuininoides* from the Early Oligocene Cethana sediments is probably related to sub-tribe Gevuininae, or the related genus *Hicksbeachia*, based on the presence of distinctive trichome bases (Carpenter and Jordan 1997).

Other Proteaceae

There are 17 species of *Euproteaciphyllum* from the Tertiary, including the earliest described proteaceous macrofossils in Tasmania. All the Tertiary fossil Proteaceae from Tasmania, except *Cenarrhenes* from Hasties, are consistent with subfamily Grevilleoideae. However the combination of hypostomaty, randomly oriented stomata, and trichome bases associated with many basal epidermal cells typical of Grevilleoideae occurs in some species from other sub-families (e.g. *Faurea* species; subfamily Proteoideae). It is likely that these characters are relatively primitive features of the family, which have subsequently been lost in the scleromorphic Proteoideae and Persoonioideae.

There are some features which are not present in any extant Proteaceae. The overlapping lobes in *E. polymorphum* are not present in any living species of Proteaceae, though this may be simply a variation on the potential range within extant Grevilleoideae. However, the longitudinal division of the subsidiary cells in this species are found in extant Proteaceae only in the very primitive *Bellendena*. Thus, there are two likely alternative interpretations of the status of *E. polymorphum*. It may be a primitive member of the Proteaceae and the similarity of the subsidiary cells to those of *Bellendena* may be plesiomorphic, or *E. polymorphum* is a member of Grevilleoideae, and the division of the subsidiary cells is a homeoplasy.

Many of the other taxa have features from a number of different groups. In particular, the lobed, toothed leaf form of many of the fossils is now common in *Lomatia*, but may in fact be a primitive trait. *Euproteaciphyllum brookerensis* has striated cuticles unlike any extant *Lomatia*, and may be a member of an extinct, primitive lineage within Grevilleoideae. Abundant highly sculpted Proteaceae pollen of a wide range of forms occur in the Early Eocene, and most of these forms were extinct by the Early Oligocene (Macphail *et al*. 1994; Martin 1995).

Biogeographic relations

In most cases where the fossils which can be assigned to living genera, their close living relatives are still present in Tasmania. Exceptions include *Hicksbeachia* and Gevuininae which are rainforest taxa mainly from Australia. *Banksieaephyllum linearis* may be of an extinct scleromorphic group of Banksieae. *Lomatia fraxinifolia* and *Orites excelsoides* are related to extant tropical/subtropical rainforest species of genera still extant in Tasmania. In contrast the *Euproteaciphyllum* species in general appear to be of groups which are extinct from Tasmania. Some, e.g. *E. polymorphum*, of these may be from higher order extinct taxa, perhaps extinct tribes or even subfamilies.

Past Diversity

Eocene

The pollen record in Tasmania prior to the Early Eocene is sparse, but suggests that regional diversity was high in the Palaeocene (e.g. Forsyth 1989), and probably the Late Cretaceous (e.g. Dettman 1994). The Eocene was a period of very high diversity of proteaceous palynomorphs (e.g. Martin 1982, 1994), but the macrofossil evidence for high species diversity is not conclusive, with

only 8-12 distinct taxa known (Table 2). This is probably due to the low number of macrofossils available, except from the as yet poorly known Regatta Point flora.

Early Oligocene

The Cethana sediments are the richest known Tasmanian site for Proteaceae with 16 taxa which can be certainly assigned to Proteaceae (Table 2), as well as other probable Proteaceae (Carpenter *et al*. 1994*a*; Carpenter and Jordan 1997). These include both mesomorphic and scleromorphic types. Four species are known from the Lemonthyme Creek core, three from the Lea River sediments, and only one from Leven River. The similarity in these numbers of proteaceous species may not reflect true diversity of Proteaceae because only about 400 macrofossils are known from Lemonthyme Creek, whereas thousands of specimens are known from Lea River. The floristics of the Early Oligocene sites are not yet thoroughly studied, and more species of Proteaceae are likely to be found, from both these and other sites. No convincing Proteaceae macrofossils have yet been found in the diverse and well-studied Little Rapid River sediments (see Carpenter *et al*. 1994*a*; Hill 1994), although one taxon has features of Proteaceae (G. J. Jordan, unpublished data).

None of the 23 proteaceous species in the four Early Oligocene sites occurs at more than one site, even though the sites are geographically close. This suggests that there were many species of Proteaceae at this time. The vegetation contributing to the fossil assemblages probably differed floristically between the four sites due to differences in the geological age, edaphics, climate or successional status of the vegetation (e.g. Hill and Scriven in press). Such floristic differentiation implies a very high regional species richness because the fossil sites almost certainly sampled only a small part of the range of environments where Proteaceae could have occurred, (e.g. only riparian, or near riparian, vegetation would have dominated the fossil floras). An alternative hypothesis is that the sites sampled vegetation with similar floristics. This hypothesis can be put in context by a statistic: it would take about 200 species to give a 50% chance of having four sites with 15, 4, 3 and 1 species respectively, without at least one species occurring at more than one site (based on a Monte Carlo simulation, e.g. Manly 1991). This value (200) is a low estimate because there are no sites at which species are shared. This suggests if there had been no differentiation in floristics, then there were probably at least 200 species of Proteaceae in north-western Tasmania in the Early Oligocene. Thus the data imply that high numbers of proteaceous species were present in Early Oligocene Tasmania, regardless of whether the floras sampled vegetation with the same floristics or not. The richness of Proteaceae may have been higher than implied above, because the fossil record tends to underestimate species richness: many species are unlikely to be fossilised, some cannot be recognised as Proteaceae, and many species cannot be differentiated from congeners using characters available in fossils. North-western Tasmania now contains only about 16 extant taxa which could be recognised as distinct Proteaceae species (Buchanan 1995; G. J. Jordan unpublished data).

Edaphic differences probably contributed to floristic differences between the sites. Carpenter and Jordan (1997) proposed that the high diversity of Proteaceae at Cethana was due to very poor soils derived from Cambrian and Precambrian metamorphosed sediments. The Leven River site probably had more fertile soils since it overlies Tertiary basalts. Lemonthyme Creek and Lea River sites are now on ancient metamorphosed sediments, but basalts occur close by. The floristics are broadly consistent with this sequence, with Cethana having a rich, mainly highly scleromorphic, proteaceous flora, the Leven River site having only a single, more mesomorphic taxon, and the other two sites having intermediate numbers of scleromorphic taxa. Climatic differences between sites may also have contributed through variation within the Early Oligocene (e.g. Macphail *et al*. 1993*a*; Quilty 1994) and altitudes differences (Hill and Scriven in press). Disturbance may have contributed, through land slippage, but fire was probably rare. Extinction and evolution of species would also contribute to site differentiation, though leaf forms, and probably species, appear to persist for a long time within the Proteaceae (e.g. Jordan 1995*a* demonstrated that many proteaceous leaf types a million years old or more were identical to extant Tasmanian species).

Late Oligocene-Pliocene

There is only one unequivocal Proteaceae taxon of this age from Tasmania , but there are only two sites known of this age (Macphail *et al*. 1991).

Pleistocene

The generic and species richness of Proteaceae in western Tasmania were probably greater in the Early Pleistocene than they are now (Jordan 1995*a*). Most of western Tasmania's extant species of Proteaceae, or very close relatives, were extant at this time, and a number of extinct forms were also present (Table 2; Jordan 1995*a*). One extinct species of Proteaceae, *Banksia kingii*, persisted until the Late Pleistocene (Jordan and Hill 1991; Jordan 1995*a*).

Implications for Past Environments and the History of Scleromorphy

Both *Euproteaciphyllum brookerensis* and *E. tasmanicum* from the Early Eocene Brooker sediments show scleromorphic features, including narrow leaflets. Their stomatal morphology would result in strong limitations to maximum stomatal conductance, restricting water loss at the expense of carbon dioxide gain since conductance is proportional to the stomatal density and increases with pore size (Jones 1992). Their stomata are typically only 15 µm and 18 µm long respectively, which is smaller than those of any extant Proteaceae measured except some highly xeromorphic *Grevillea* (Table 3). They also have relatively few stomata and the apertures in the outer cuticle ledges of *E. brookerensis* are very narrow (Fig. 25). The Early Eocene Buckland Proteaceae and the several species of Proteaceae in the Late Palaeocene Lake Bungarby sediments from mainland Australia also have very small stomata (G. J. Jordan, unpublished data). In particular, *Banksieaephyllum taylorii* R.J.Carp., G.J.Jord. & R.S.Hill has smaller stomata (about 15-18 µm long) than any extant *Banksia* or *Dryandra* (Table 3). The Early Oligocene *Banksieaephyllum linearis* and *B. orientalis* from Cethana also have very small stomata (15 and 20 µm respectively). The stomata of some of the other Cethana Proteaceae are small, but not exceptionally so (18-25 µm), but those of the other Early Oligocene Proteaceae tend to be similar in size to many extant members of the family.

Thus there appears to be a strong trend from very small stomata in Proteaceae in the earliest Tertiary to larger ones later. This may be related to very high atmospheric CO_2 concentration in the earliest Tertiary, followed by a general trend to decline (e.g. Berner 1990). Stomatal index certainly appears to have responded in some species to changes in atmospheric CO_2 concentration over the Neogene (e.g. Woodward and Kelly 1995; Kurschner 1996). The response of maximum stomatal conductance is less clear (e.g. Kurschner 1996), but limitation to conductance may have been favoured under these conditions because increased atmospheric CO_2 concentration reduces the amount of total diffusion required for the diffusion of a given amount of CO_2 into a leaf. If photosynthesis is limited (e.g. by nutrient availability, temperature or low light), and there were periods of mild or severe water stress, then restriction of gas exchange would be favoured. Possible contributing factors would be very low nutrients at some sites, and low light intensity due to high latitude and cloud (e.g. Hill and Scriven 1995), or understorey habits. Stomatal size is also related to ploidy level and Masterson (1994) explained trends in increasing guard cell length in terms of changes in ploidy level. This does not preclude a relationship with changing atmospheric CO_2 concentration, but Masterson's (1994) hypothesis fits poorly with the data for Proteaceae, especially the Persoonioideae which all have long guard cells (Table 3) but generally have low chromosome numbers (Johnson and Briggs 1975). The small stomata are not likely to be due to dry climates. Conditions at the time of deposition are unlikely to have been dry in the area because the Early Eocene is generally considered to be among the wettest and warmest periods of the Cenozoic, with much rainforest in Australia (e.g. Macphail *et al*. 1994). The cuticles have features suggesting wet conditions: abundant, well developed epiphyllous fungal germlings which probably indicate wet conditions (e.g. Lange 1976), and striated cuticles (e.g. Carpenter 1994). In addition, mesomorphic species of Proteaceae often have smaller stomata than their relatives from dry climates (e.g. the rainforest Musgraveinae have smaller stomata than the Banksiinae, Table 3). A more comprehensive study of stomatal size and frequency in extant and fossil Proteaceae is required to

confirm these trends and determine their magnitude.

The divergence of Proteaceae into scleromorphic and mesomorphic forms had occurred independently in several lineages by the Early Oligocene. *Orites scleromorpha*, *O. milliganoides* and *Lomatia xeromorpha* were very scleromorphic. However, much less scleromorphic congeners, *Lomatia fraxinifolia* and *Orites excelsoides*, were also present. Both scleromorphic and mesomorphic Banksieae have also been present since the very early Tertiary (Christophel 1984; Hill and Christophel 1988; Carpenter *et al* 1993*a*, *b*; Hill 1994). Most of the known Proteaceae in Tasmanian Early Oligocene sediments have scleromorphic features, with some showing other features such as stomatal protection. Most species have small, narrow or finely divided leaves, and most have thick cuticle. Only *Orites excelsoides* and *Lomatia fraxinifolia* are convincingly mesomorphic. Mesomorphic taxa may have been more abundant in the vegetation because the processes of fossilisation can be biased against large leaves with less supportive tissue.

The ecological roles of some of the Early Oligocene scleromorphic taxa may have resembled that of the extant species *Orites milliganii*, which occurs in the subalpine or alpine equivalent of rainforest (undisturbed woody vegetation of very wet and cold climates). *Orites milliganii* is slow growing, its reproduction is largely vegetative, it is very long lived, but can survive only mild fires. It is the nearest living relative of two of the Lea River species. These three *Orites* species are highly scleromorphic, with very thick, hard, small leaves and very thick cuticle. The hypodermi in these species have two significant ecological effects. They provide mechanical support in an environment with frequent strong winds and ice abrasion, and reduce the amount of light reaching the mesophyll, which is significant because high light intensity can be highly stressful in cold environments. The papillose abaxial surface and narrow, entire revolute margined leaves of *E. papillosum* from Lea River are also consistent with subalpine rainforest. All but one, *Kermadecia pronyensis*, of the taxa with papillae are restricted to cool, wet climates, and the papillae have arisen convergently several times, suggesting that they are adaptive. The leaf form is very prominent in evergreen subalpine woody vegetation.

Early Oligocene Tasmanian macrofloras (e.g. Carpenter *et al*. 1994*a*) have many floristic similarities to Tasmanian subalpine rainforest, which is dominated by conifers, *Nothofagus gunnii* and *N. cunninghamii*, and scleromorphic Epacridaceae and Proteaceae, including other *Orites* species, *Telopea truncata* and *Lomatia*. This vegetation type extends to relatively low altitudes in ever wet glacial refugia, suggesting that it could occur in slightly warmer climates, provided rainfall was high enough. Cool or cold, ever wet, undisturbed vegetation is, therefore, a plausible site of origin and/or diversification of some groups of scleromorphic Proteaceae, notably the scleromorphic Embothrieae, Oriteae and Banksiinae.

There is little macrofossil evidence for the presence in the Early Tertiary of southern Australia of the Grevilleae, Persoonioideae and Proteoideae (Carpenter *et al.* 1994*b*), which are the groups most rich in extant scleromorphic species. The relevant genera, and possibly subgeneric groups, may have arisen in the Late Cretaceous or Early Tertiary (e.g. Johnson and Briggs 1975; Dettmann and Jarzen 1991) but the general drying of climates in southern Australia since the Miocene (Bowler 1982) probably prompted massive speciation in these groups. Thus Memon (1984) recorded a marked post-Pliocene increase in pollen surface types, attributed largely to *Grevillea* and *Hakea*, and most extant species occur in seasonally dry climates (e.g. Wrigley and Fagg 1981; Vogts 1982; McCarthy 1995). However, it is possible that these groups were speciose in the Early Tertiary, but are merely poorly recorded in the fossil record, because leaves from shrubs and from dry climates are unlikely to reach potential fossil sites. Carpenter *et al.* (1994*b*) proposed a long history for this shrubby habit, and drier areas may well have been present in central Australia in the Early Tertiary (Hill 1994). Some impression fossils from western, central and northern Australia have leaf form consistent with *Grevillea* (e.g. Pole and Bowman 1996; McLoughlin and Hill 1996), but their lack of cuticles means that there is uncertainty in their status as Proteaceae, and especially as Grevilleae. Early Tertiary Proteaceous macrofossils from south-western Australia do not seem to have affinity with Grevilleae, Persoonioideae or Proteoideae, whereas some can be assigned to Embothrieae, and appear to be associated with moderately wet climates (Hill and Merrifield 1993; Carpenter and Pole 1995). In Africa, Midgley (1987) argued for a diversification of African

Proteaceae in arid, or semi-arid conditions, though there is little evidence for his postulate for an arid temperate origin for the family as a whole.

Thus scleromorphic groups appear to have followed two trends: the groups associated with more wet climates (Embothrieae and Oriteae) appear to have been very species rich in the Early Tertiary and suffered massive extinction, but there is little evidence in the Tertiary of Grevilleae, Persoonioideae and Proteoideae, which are now very species rich. Banksiinae may have followed both trends, with decline in some groups, and speciation of others, especially in south-western Australia.

Acknowledgments

We thank Katie Dutch for the line drawings, Leonie Scriven for some Lea River specimens, Eric Colhoun for the Lemonthyme Creek core, and the Royal Tasmanian Botanic Gardens for some living Proteaceae. This work was supported by an Australian Research Council large grant to R.S.H., and an Australian Research Council postdoctoral fellowship to G.J.J.

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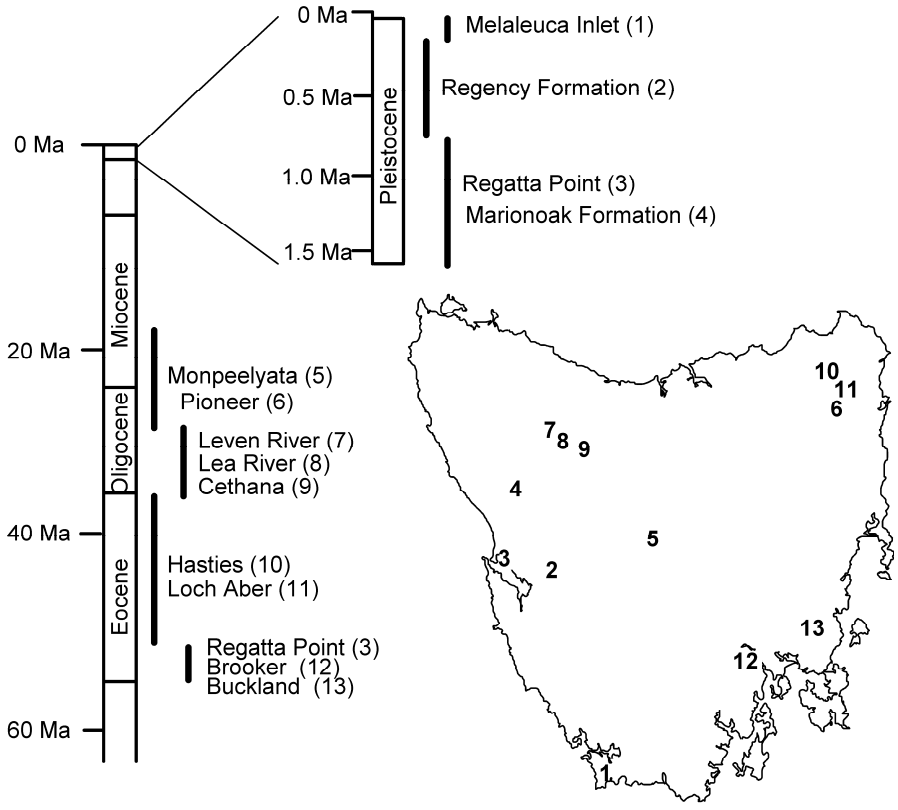
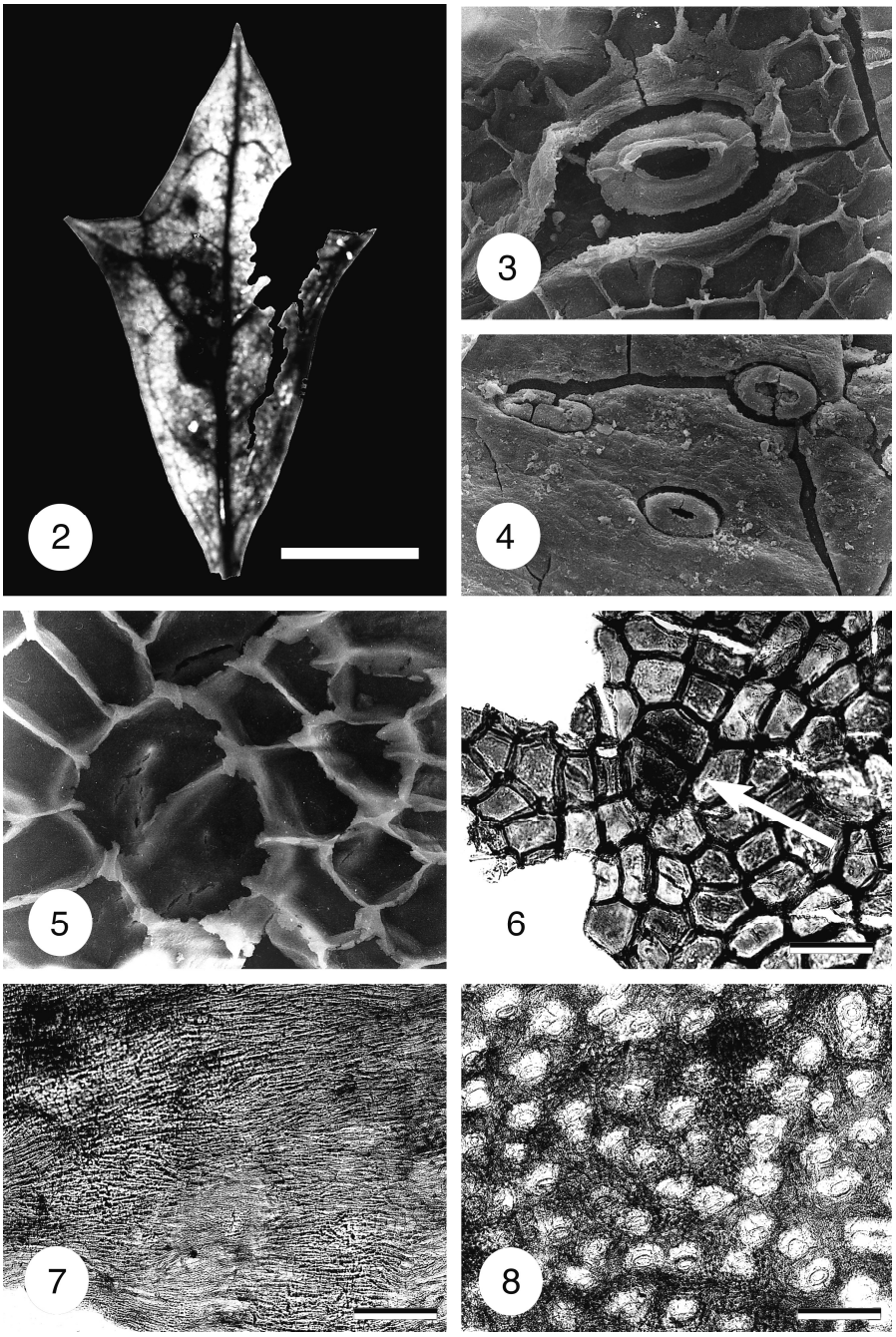
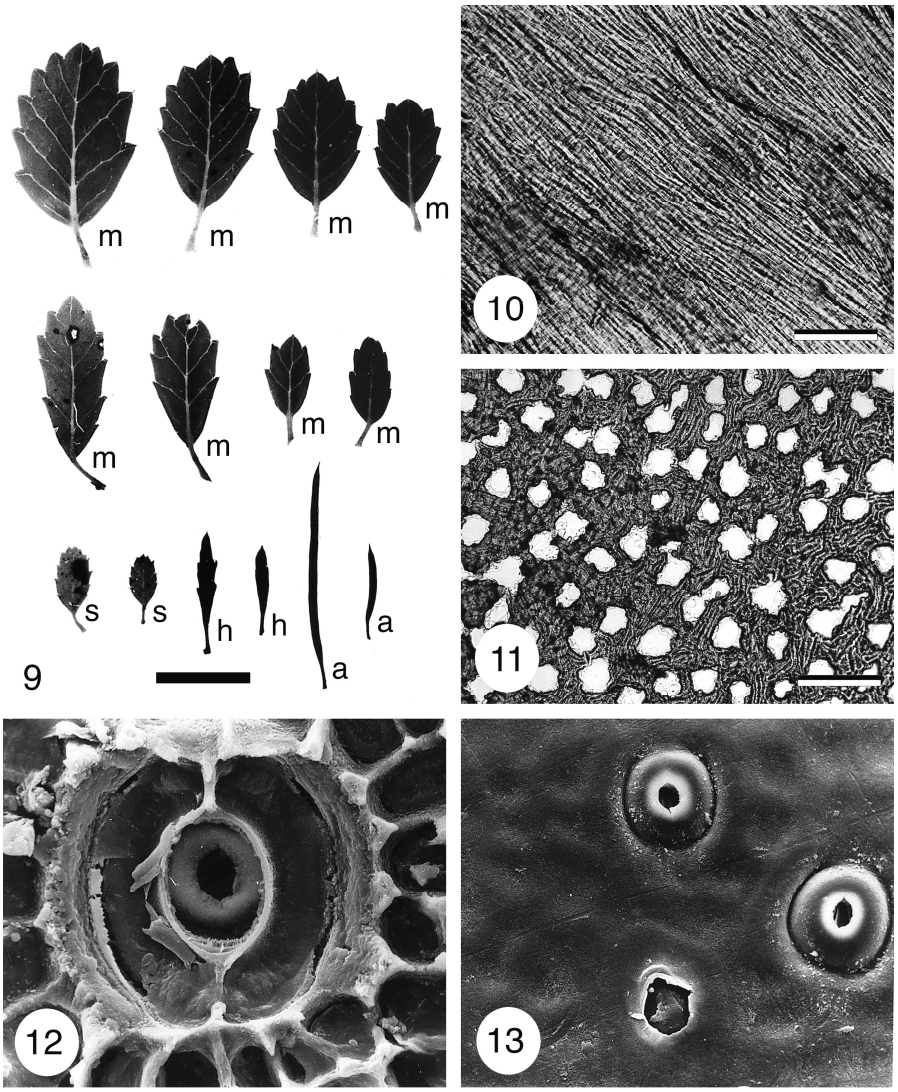


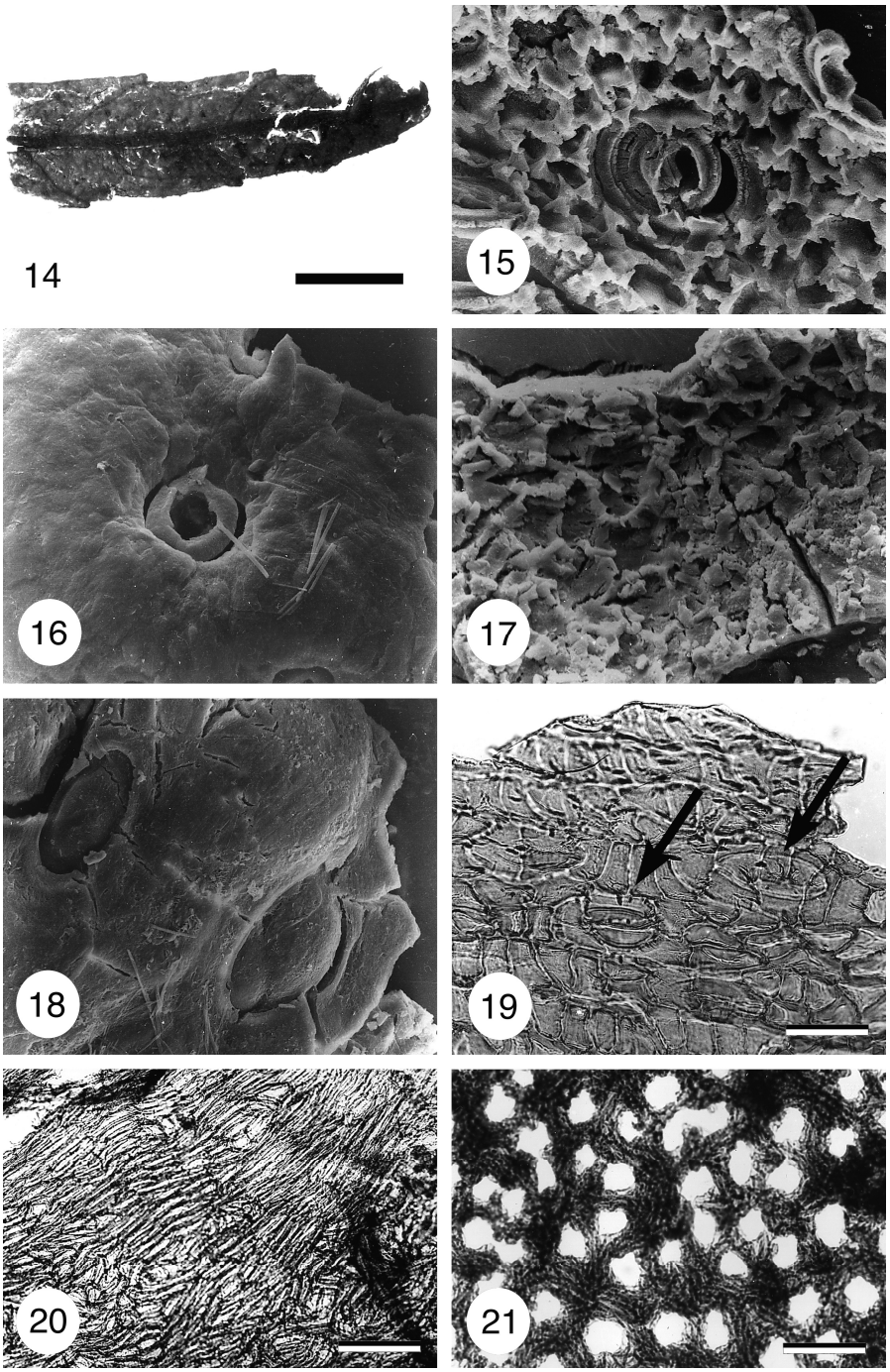
Fig. 1. Age and location of fossil deposits in Tasmania discussed in this work. Time scale is based on Harland *et al*. (1990). Ages of sites are explained in text. Note that Regatta Point has both Early Eocene and Early Pleistocene fossil bearing sediments.



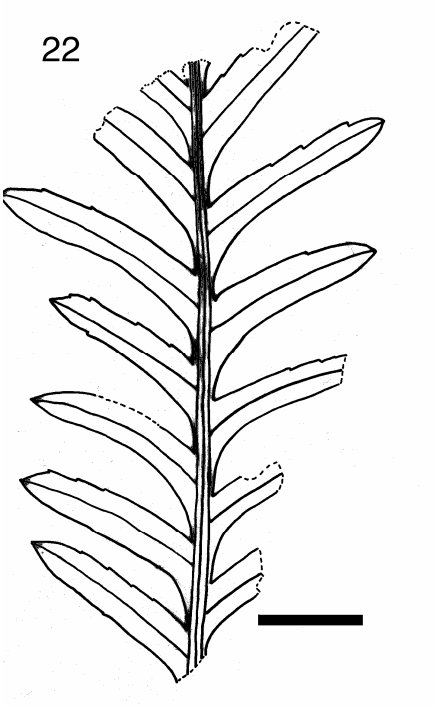
Figs 2-8. Holotype of *Orites milliganoides* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (Lea2550). **Fig. 2.** Partially cleared, mummified leaf. Scale = 5 mm. **Figs 3-5.** Scanning electron micrographs (SEMs) of cuticle. **Fig. 3.** Inner surface of abaxial surface showing a large stoma and small epidermal cells. x430. **Fig. 4.** Outer surface of abaxial surface showing stomata slightly depressed into otherwise smooth cuticle surface. x490. **Fig. 5.** Inner surface of adaxial surface. x450. **Fig. 6.** Light micrograph (LM) of adaxial surface showing a trichome base (arrow). scale = 50 µm. **Fig. 7**. LM of hypodermis of adaxial surface. Scale = 200 µm. **Fig. 8.** LM of hypodermis of abaxial surface. Scale = 200 µm.



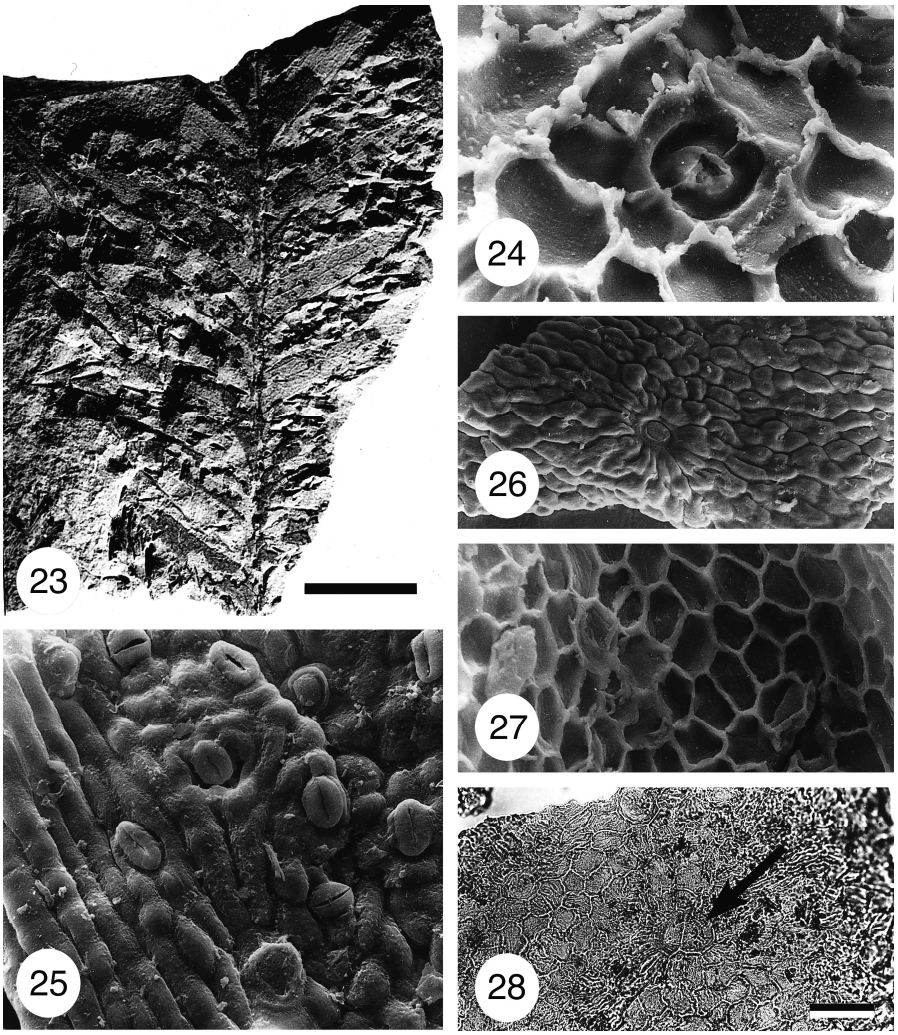
Figs 9-13. Extant *Orites* species. **Fig. 9.** Variation in gross leaf form of some *Orites* species: adult leaves of *O. milliganii* (m), seedling leaves of *O. milliganii* (s), adult leaves of a putative hybrid between *O. milliganii* and *O. acicularis* from Mt Read, western Tasmania (h), and adult leaves of *O. acicularis* (a). Scale = 20 mm. **Fig. 10**. LM of hypodermis of adaxial surface of *O. milliganii*. S cale = 200 µm. **Fig. 11.** LM of hypodermis of abaxial surface of *O. milliganii*. Scale = 200 µm. **Figs 12 and 13.** SEMs of cuticle of *O. acicularis*. Compare with Figs 3, 4, 15 and 16. **Fig. 12.** Inner surface of abaxial surface. x750. **Fig. 13.** Outer surface of abaxial surface. x350.



Figs 14-21. Holotype of *Orites scleromorpha* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (Lea1554). **Fig. 14.** Partially cleared, mummified leaf. Scale = 5 mm. **Figs 15-18** SEMs of cuticle. **Fig. 15.** Inner surface of abaxial surface showing a large stoma and small epidermal cells. x450. **Fig. 16.** Outer surface of abaxial surface showing a stoma slightly depressed into otherwise smooth cuticle surface. x450. **Fig. 17.** Inner surface of adaxial surface. x430. **Fig. 18.** Outer surface of adaxial surface showing two trichome bases. x430. **Fig. 19.** LM of adaxial surface showing trichome bases (arrows). Scale = 50 µm. **Fig. 20**. LM of hypodermis of adaxial surface. Scale = 200 µm. **Fig. 21.** LM of hypodermis of abaxial surface. Scale = 200 µm.



Figs 22. Holotype of *Euproteaciphyllum brookerensis* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (BH1). Scale = 10 mm.



Figs 23-28. Holotype of *Euproteaciphyllum brookerensis* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (BH1). **Fig. 23.** Compression of leaf. Scale = 10 mm. **Figs 24-27.** SEMs of cuticle. **Fig. 24.** Inner surface of abaxial surface showing a small stoma. x875. **Fig. 25.** Outer surface of abaxial surface showing the stomata with cuticular ledges with narrow apertures and raised well above the cuticle surface. x415. **Fig. 26.** Outer surface of adaxial surface showing the ornamentation creating a striated appearance under light micrography. x210. **Fig. 27.** Inner surface of adaxial surface. x480. **Fig. 28.** LM of adaxial surface showing a trichome bases (arrow). Scale = 50µm.

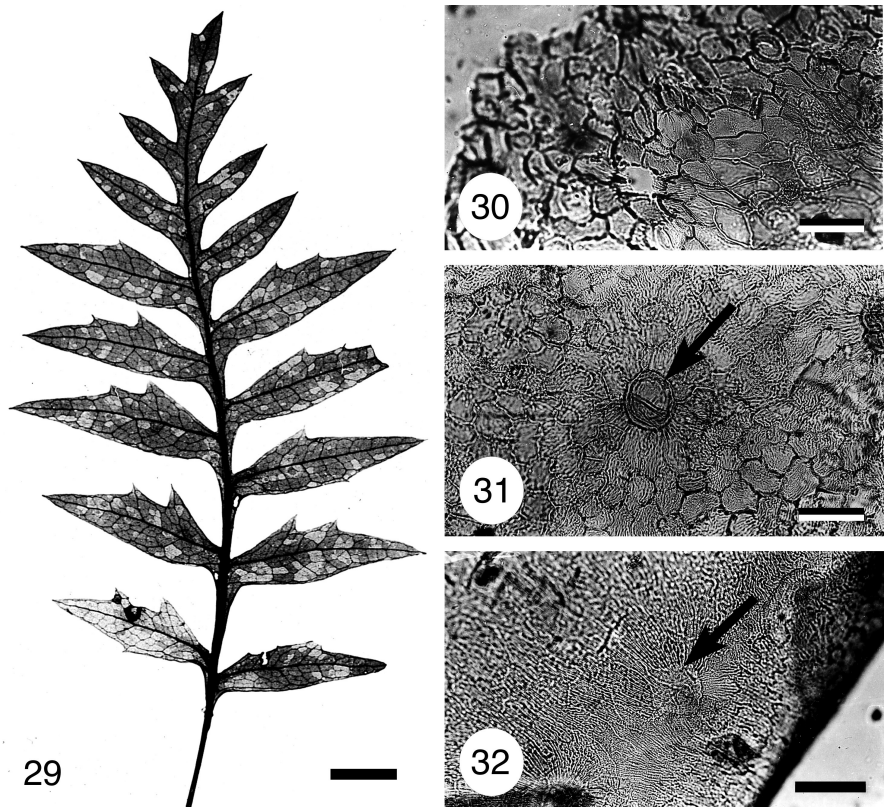


Fig. 29. Leaf of *Lomatia fraseri*. Scale = 10 mm. **Figs 30-32.** LMs of cuticles of Proteaceae from Buckland. **Fig. 30.** Abaxial surface of specimen 1 (cf. *E. brookerensis*). Scale = 50 µm. **Fig. 31.** Adaxial surface of specimen 2 (cf. *E. brookerensis*) showing a trichome base (arrow). Scale = 50 µm. **Fig. 32.** Adaxial surface of specimen 3 showing a trichome base overlying two cells (arrow). Scale = 50 µm.

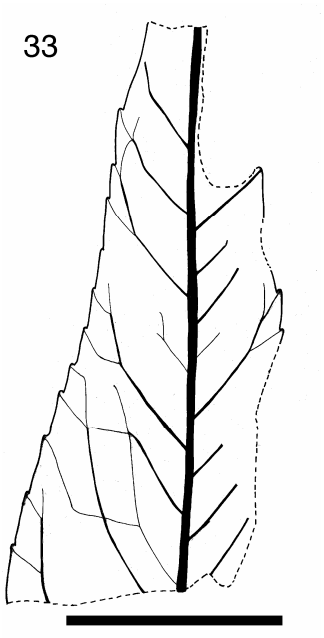
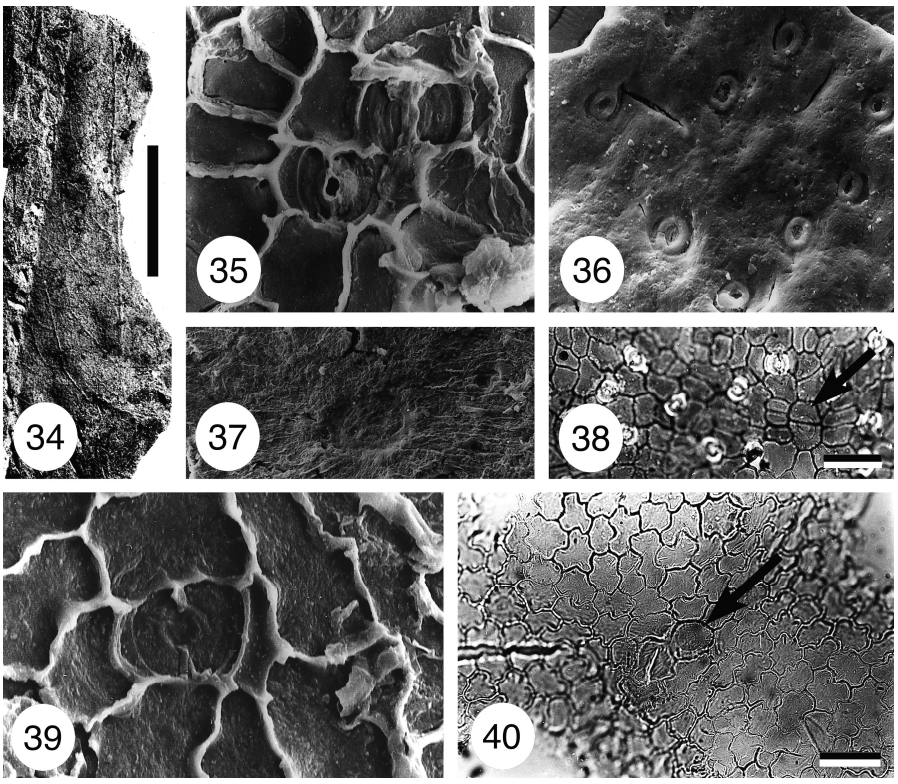
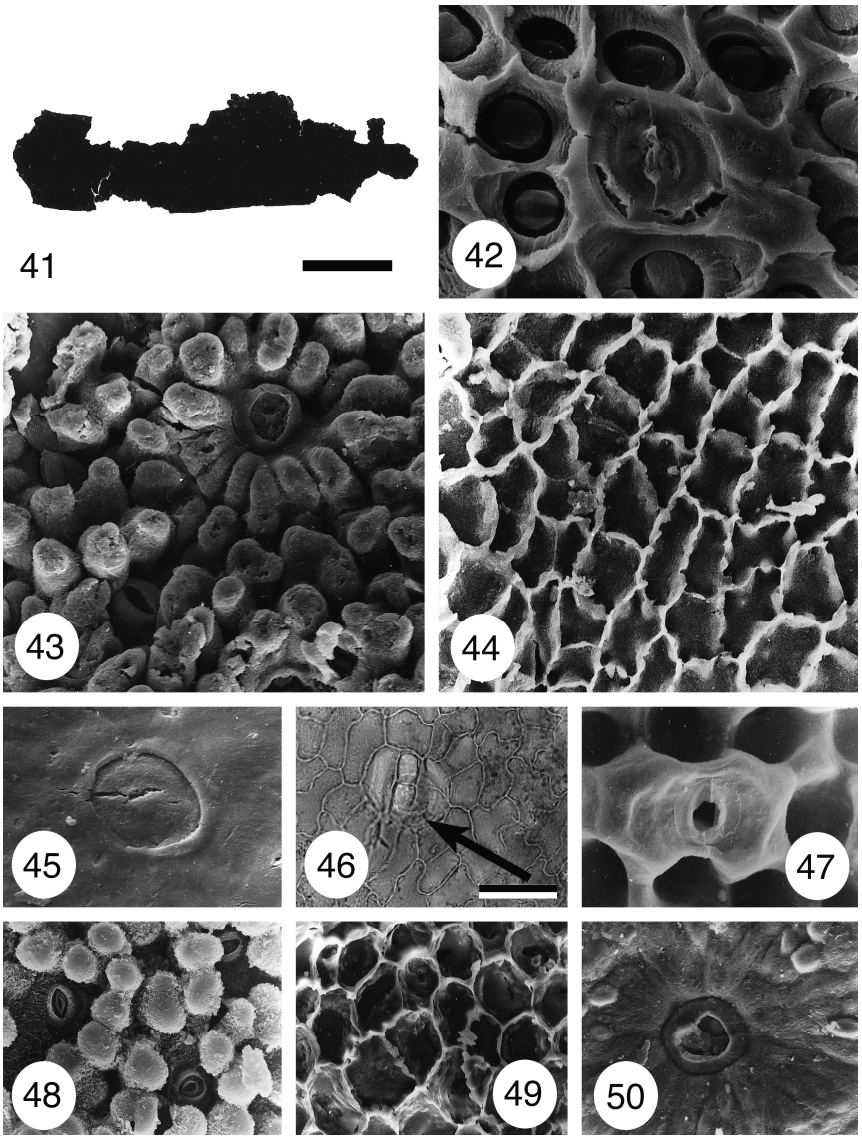


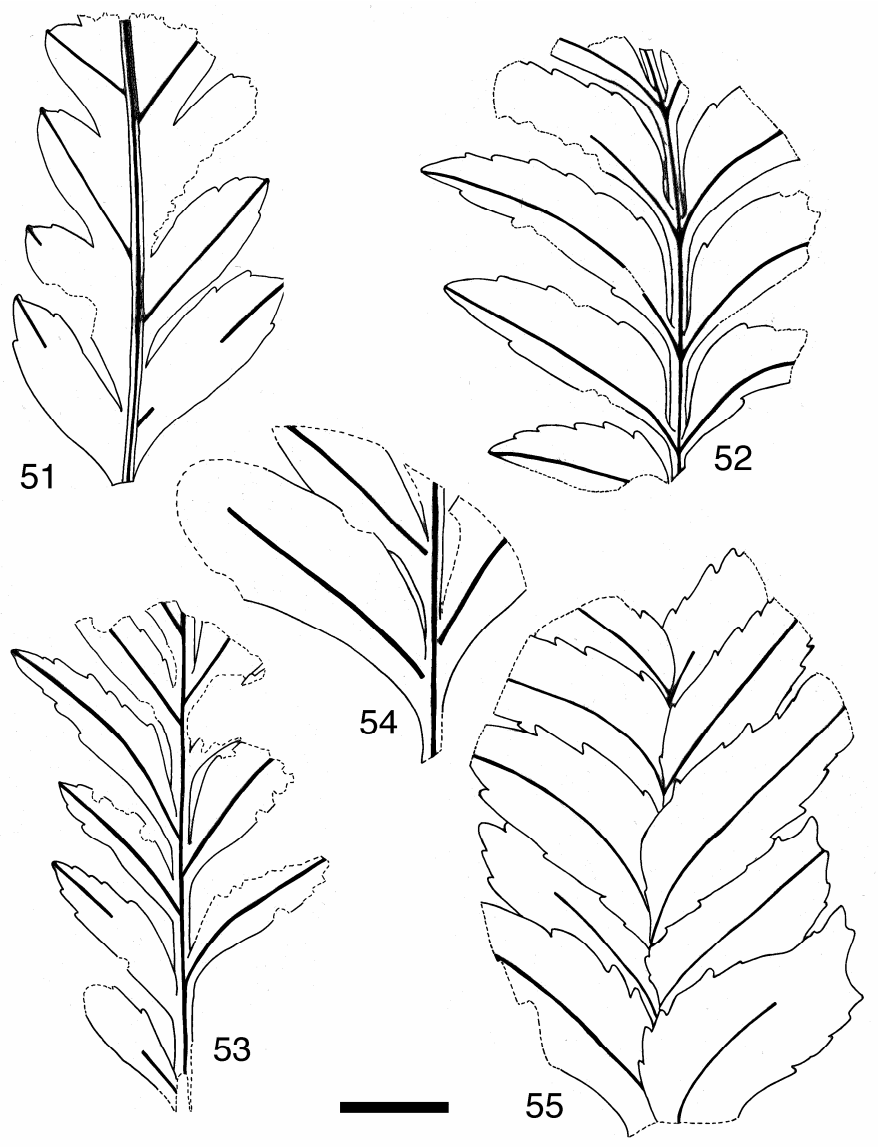
Fig. 33. Holotype of *Euproteaciphyllum tasmanicum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (BH11). Drawn from part and counterpart. Scale = 10 mm.



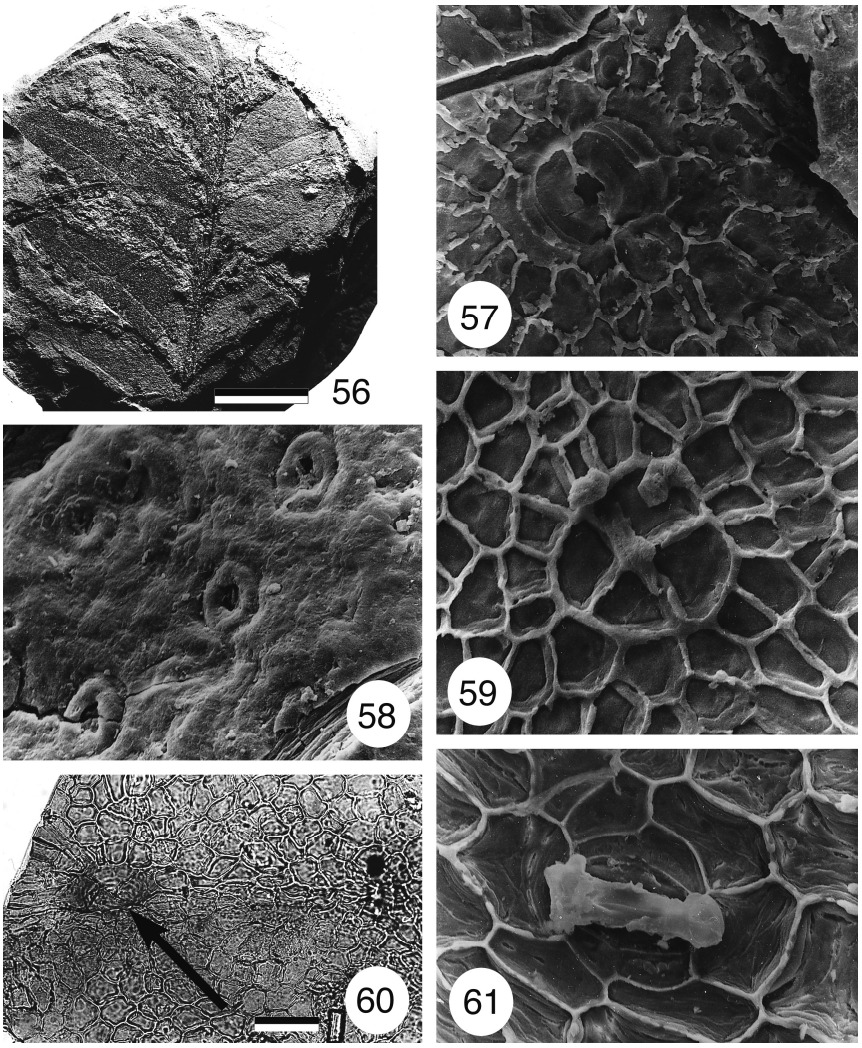
Figs 34-40. Holotype of *Euproteaciphyllum tasmanicum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (BH11; Figs 34-38), and a specimen possibly attributable to *E. tasmanicum* (BH5; Figs 39-40). **Fig. 34.** Compression of leaf. Scale = 10 mm. **Figs 35-37.** SEMs of cuticle. **Fig. 35.** Inner surface of abaxial surface showing two small stomata. x715. **Fig. 36.** Outer surface of abaxial surface showing slightly depressed, sparse stomata. x370. **Fig. 37.** Outer surface of adaxial surface. x380. **Fig. 38.** LM of abaxial surface showing a trichome bases (arrow). Scale = 50 µm. **Fig. 39.** SEM of inner surface of cuticle of abaxial surface. x1160. **Fig. 40.** LM of adaxial surface showing a trichome bases (arrow). Scale = 50 µm.



Figs 41-50. Holotype of *Euproteaciphyllum papillosum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (Lea1762; Figs 41-46), and *Lomatia ferruginea* (Sydney Botanic Gardens accession number 876767; Figs 47-50). **Fig. 41.** Mummified leaf. Scale = 5 mm. **Figs 42-45.** SEMs of cuticle. **Fig. 42.** Inner surface of abaxial surface showing a stoma. Note that each papilla is formed by only part of the periclinal wall of an epidermal cell. x825. **Fig. 43.** Outer surface of abaxial surface showing a trichome base, and papillae protecting the stomata. x420. **Fig. 44.** Inner surface of adaxial surface. x460. **Fig. 45.** Outer surface of adaxial surface showing the smooth surface and a trichome base. x420. **Fig. 46.** LM of adaxial surface showing a trichome base (arrow). Scale = 50 µm. **Figs 47-50.** SEMs of cuticle of *L. ferruginea*. Compare with Figs 42-45. **Fig. 47.** Inner surface of abaxial surface showing a stoma. Note that each papilla is formed by all of the periclinal wall of an epidermal cell. x590. **Fig. 48.** Outer surface of abaxial surface. x290. **Fig. 49.** Inner surface of adaxial surface. x260. **Fig. 50.** Outer surface of adaxial surface. x270.



Figs 51-55. Variation in *Euproteaciphyllum polymorphum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. **Fig. 51.** LT137, showing lobed apical leaf region. **Fig. 52.** LT337 (holotype). Note the attachment of the upper margin to near the centre of the midrib, and the apparently long decurrent basal margin. Drawn from part and counterpart. **Fig. 53.** LT344. Drawn from part and counterpart. **Fig. 54.** LT022 showing partial overlapping of leaflets. **Fig. 55.** LT343 showing strongly overlapping leaflets. Reconstructed from dissection of part and counterpart. Scale bar = 10 mm.



Figs 56-61. Holotype of *Euproteaciphyllum polymorphum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT337; Figs 51-60) and *Bellendena montana* (Fig. 61). **Fig. 56.** Compression of leaf. Scale = 10 mm. **Figs 57-59.** SEMs of cuticle. **Fig. 57.** Inner surface of abaxial surface showing a stoma. Note the septum across one of the subsidiary cells, and the small epidermal cells. x210. **Fig. 58.** Outer surface of abaxial surface showing relatively smooth surface and slightly sunken stomata. x400. **Fig. 59.** Inner surface of adaxial surface showing the differentiated basal epidermal cells of a trichome base. x240. **Fig. 60.** LM of adaxial surface showing a trichome base (arrow). Scale = 20 µm. **Fig. 61.** SEM of cuticle of *Bellendena montana*. Note the separated subsidiary cells. x420.

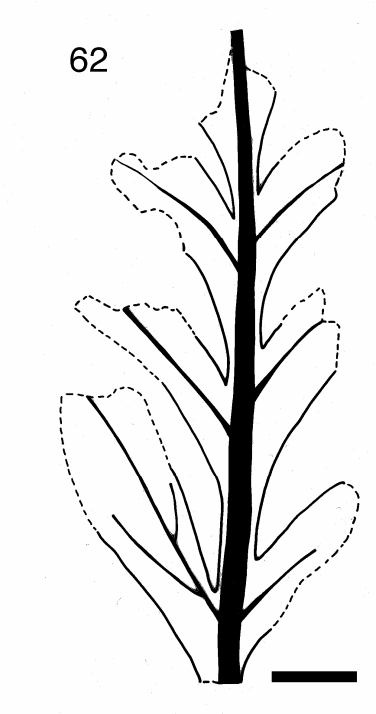
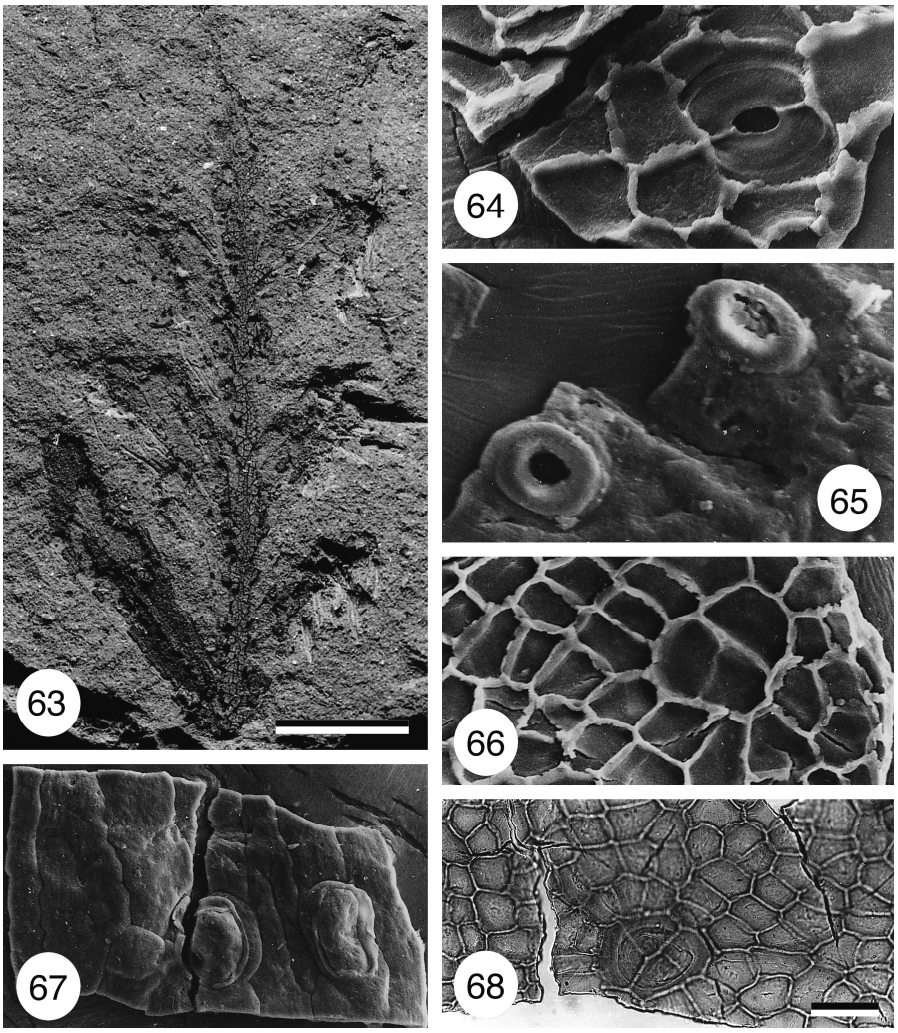


Fig. 62. Holotype of *Euproteaciphyllum microlobium* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT310). Drawn from part and counterpart. Scale = 5 mm.



Figs 63-68. Holotype of *Euproteaciphyllum microlobium* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT310). **Fig. 63.** Compression of leaf. Scale = 5 mm. **Figs 64-67.** SEMs of cuticle. **Fig. 64.** Inner surface of abaxial surface showing a stoma. x520. **Fig. 65.** Outer surface of abaxial surface. x510. **Fig. 66.** Inner surface of adaxial surface showing the differentiated basal epidermal cells of a trichome base. x280. **Fig. 67.** Outer surface of adaxial surface. x280. **Fig. 68.** LM of adaxial surface showing an obvious trichome base. Scale = 50 µm.

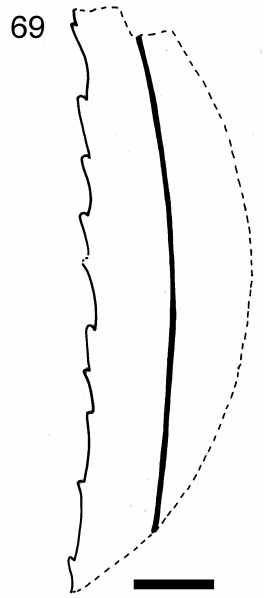
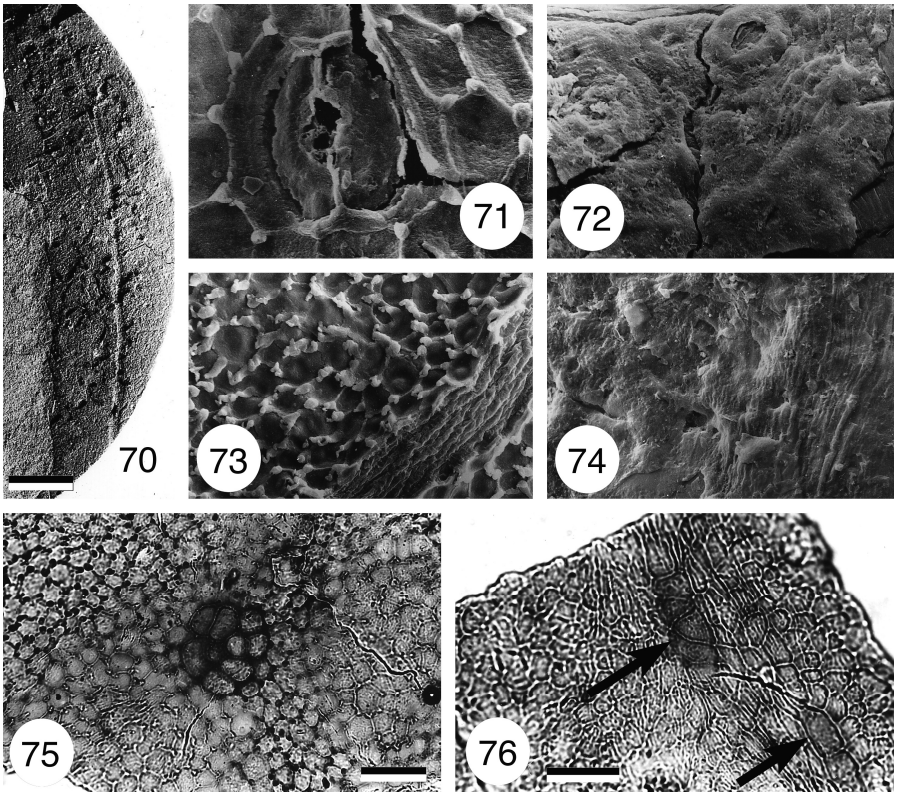
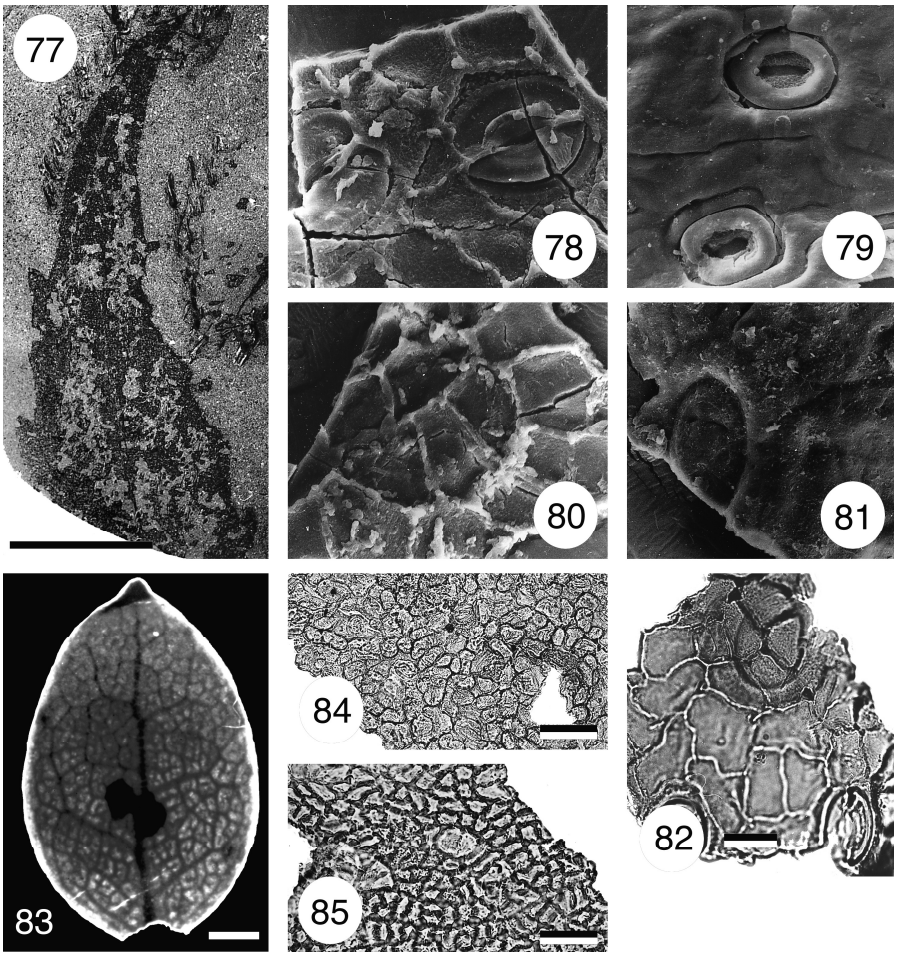


Fig. 69. Holotype of *Euproteaciphyllum falcatum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT194). Scale = 5 mm.



Figs 70-76. Holotype of *Euproteaciphyllum falcatum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT194). **Fig. 70.** Compression of leaf. Scale = 5 mm. **Figs 71-74.** SEMs of cuticle. **Fig. 71.** Inner surface of abaxial surface showing a stoma. x760. **Fig. 72.** Outer surface of abaxial surface. The cuticle is degraded but striations near the stoma are visible. x445. **Fig. 73.** Inner surface of adaxial surface. Note the isodiametric laminar epidermal cells, and elongate cells associated with a vein. x380. **Fig. 74.** Outer surface of adaxial surface. Note the longitudinal striations on part of the fragment. x400. **Figs 75 and 76.** LMs of lamina of adaxial surface. **Fig. 75.** Lamina region. Note the large trichome base. Scale = 50 µm. **Fig. 76.** Veinal region. Note the elongate trichome bases (arrows) and longitudinal striations. Scale = 50 µm.



Figs 77-82. Holotype of *Euproteaciphyllum serratum* G.J.Jord., R.J.Carp. & R.S.Hill sp. nov. (LT201). **Fig. 77.** Compression of leaf. Scale = 10 mm. **Figs 78-81.** SEMs of cuticle. **Fig. 78.** Inner surface of abaxial surface showing a stoma. x470. **Fig. 79.** Outer surface of abaxial surface showing slightly sunken stomata. x390. **Fig. 80.** Inner surface of adaxial surface. x400. **Fig. 81.** Outer surface of adaxial surface. x400. **Fig. 82.** LM of abaxial surface. Note the obvious, large trichome base. Scale = 50 µm. **Figs 83-85.** Monpeelyata Proteaceae species. **Fig. 83.** Mummified leaf. Scale = 2 mm. **Fig. 84.** LM of abaxial surface. Scale = 50 µm. **Fig. 85.** LM of adaxial surface. Note trichome base (arrow). Scale = 50 µm.